

Three new *Russula* species in sect. *Ingratae* (Russulales, Basidiomycota) from southern China

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Academic editor: Alfredo Vizzini | Received May 2021 | Accepted 4 October 2021 | Published 8 November 2021

Citation: Li G-J, Li S-M, Buyck B, Zhao S-Y, Xie X-J, Shi L-Y, Deng C-Y, Meng Q-F, Sun Q-B, Yan J-Q, Wang J, Li M (2021) Three new *Russula* species in sect. *Ingratae* (Russulales, Basidiomycota) from southern China. MycoKeys 84: 103–139. <https://doi.org/10.3897/mycokeys.84.68750>

Abstract

Three new species of *Russula* section *Ingratae*, found in Guizhou and Jiangsu Provinces, southern China, are proposed: *R. straminella*, *R. subpectinatoides* and *R. succinea*. Photographs, line drawings and detailed morphological descriptions for these species are provided with comparisons against closely-related taxa. Phylogenetic analysis of the internal transcribed spacer (ITS) region supported the recognition of these specimens as new species. Additionally, *R. indocatillus* is reported for the first time from China and morphological and phylogenetic data are provided for the Chinese specimens.

Keywords

Agaricomycetes, ITS, morphology, phylogeny, Russulaceae, taxonomy

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Introduction

Russula Pers. is a widespread genus that contains at least 2000, but possibly as many as 3000 species worldwide (Li et al. 2018; Adamčík et al. 2019; He et al. 2019). Members of this genus form symbiotic relationships with a diversity of plant species in broad-leaved and coniferous forests, scrubland and meadows. The brightly tinged pileus, abundant sphaerocytes responsible for the fragile gills and stipe, amyloid spore ornamentation, gleocystidia staining in sulpho-aldehydes, lack of clamp connections and absence of a ramifying lactifer system ending in pseudocystidia are the main morphological features of this genus (Li et al. 2015a; Buyck et al. 2018; Looney et al. 2018). Due to frequent convergence or extreme plasticity of morphological features, precise identification of *Russula* species is difficult and establishing accurate taxonomy is challenging (Miller and Buyck 2002; Bazzicalupo et al. 2017).

Russula sect. *Ingratae* Quél. is characterised by tawny, ochraceous or ashy-grey to dark brown pileus with tuberculate striate margin, acute to subacute equal lamellae, flesh with a distinct fetid, spermatic or waxy odour, or like bitter almonds, cream-coloured spore print, spores partly showing inamyloid reaction in the suprahilar area, small- to medium-sized unicellular pileocystidia and articulated and branched hyphal ends in the pileipellis (Shaffer 1972; Romagnesi 1985; Sarnari 1998). The combination of these characters makes this section one of the more easily distinguishable groups in the *Russula* subgenus *Heterophyllidiae* Romagn. Recent multi-locus phylogenetic studies indicated that this morphologically well-defined group corresponded to the earlier subsections, *Foetentinae*, *Pectinatinae* and *Subvelatae*, representing a natural, well-supported monophyletic clade in phylogenetic topology of the northern temperate region (Looney et al. 2016; Buyck et al. 2018). The other easily distinguishable groups of subgenus *Heterophyllidiae* include subsections *Amoeninae*, *Virescentinae* and *Substriatinae*. Phylogenetic analyses also indicated it is more difficult to match a field aspect with a single monophyletic lineage (Wang et al. 2019; Deng et al. 2020; Wisitrassameewong et al. 2020).

Compared with Europe (Romagnesi 1985; Sarnari 1998), detailed analyses of *Russula* sect. *Ingratae* in Asia began relatively late. In southern China, several species were previously misidentified, based on morphological characters, with European or North American names, such as *R. foetens* Pers., *R. grata* Britzelm. (= *R. laurocerasi* Melzer) and *R. pectinatoides* Peck (Song et al. 2007; Li 2014). Rapid progress has been made in the past two decades, resulting in 15 new *Russula* species in Asian *Ingratae*, based on modern phylogenetic methods: *R. abbotensis* K. Das & J.R. Sharma, *R. ahmadii* Jabeen et al., *R. arunii* S. Paloi et al., *R. catillus* H. Lee et al., *R. dubdiana* K. Das et al., *R. foetentoides* Razaq et al., *R. gelatinosa* Y. Song & L.H. Qiu, *R. indocatillus* Ghosh et al., *R. natarajanii* K. Das et al., *R. obscuricolor* K. Das et al., *R. pseudocatillus* F. Yuan & Y. Song, *R. pseudopectinatoides* G.J. Li & H.A. Wen, *R. rufobasalis* Y. Song & L.H. Qiu, *R. subpunctipes* J. Song and *R. tsokae* K. Das et al. These new species were originally described from East Asia and the adjacent Himalayan area (Das et al. 2006, 2010, 2013, 2017; Razaq et al. 2014; Li et al. 2015b; Jabeen et al. 2017; Lee et al. 2017; Song et al. 2018, 2020; Ghosh et al. 2020). The initial sequence data have supported the valid

recognition of *R. punctipes* Singer and *R. senecis* Imai, but are still lacking for *R. guangdongensis* Z.S. Bi & T.H. Li and *R. periglypta* Berk & Broome (Lee et al. 2017; Song et al. 2018). Recent rDNA ITS phylogenetic analyses of *R. sect. Ingratae* in the Northern Hemisphere showed numerous unknown taxa and constant misidentifications of species in this group (Avis 2012; Melera et al. 2017; Park et al. 2017).

The importance of precise identification of *Russula* spp. in sect. *Ingratae* also comes from their economic value as several species are commonly sold as edible fungi in markets of southern China under the local name “You-la-gu (oily, acrid mushroom)”. Several species of *R. sect. Ingratae* may cause gastrointestinal problems if not properly pre-cooked (Dai et al. 2010; Bau et al. 2014; Chen et al. 2016). During recent years, several field investigations have been carried out on campuses and, in parks, natural reserves and wild mushroom markets of south-western China to unveil the species diversity of sect. *Ingratae* in this region. A number of *Russula* taxa have been discovered as new to science, based on morphological and molecular phylogenetic evidence, of which three members of *R. sect. Ingratae* are described and illustrated herein. Additionally, we report *R. indocatillus* as a new record for China.

Materials and methods

Morphological analyses

Specimens were collected in Guizhou, Jiangxi and Jiangsu Provinces from July to September in 2017 and 2018. The majority of the samplings are from Guizhou Province of south-western China. This mountainous Province lies in the eastern end of the Yungui Plateau. This region has a humid subtropical monsoon climate and is mostly covered by subtropical evergreen forests (Editorial Board of Vegetation in China 1980; Chen et al. 2020). Each of the specimens was collected from different patches of forest to avoid duplications from a single mycelium. Photographs of fresh basidiocarps were taken using a Canon Powershot G1 X Mark II digital camera in the field. Macroscopic characters were recorded at the same time under daylight. The colour codes and names from Ridgway (1912) were employed in descriptions. Specimen desiccation was accomplished in a Fruit FD-770C food dryer at a constant temperature of 65 °C over 12 h. Small tissue pieces of lamellae and pileipellis for microscopic observations were taken from dried specimens, sectioned by hand with a Dorco razor blade and rehydrated in 5% potassium hydroxide (KOH). Microscopical characters were observed using a Nikon Eclipse Ci-L photon microscope and Olympus BH2 with a drawing tube. Staining of basidiospores, mycelia and cystidia were performed by chemical reaction with Melzer’s Reagent and sulphovanillin (SV). Measurements and line drawings of basidiospores (exclusive of apiculus and spore ornamentation) and elements in hymenium, pileipellis and stipitipellis were executed from microphotographs taken at 1600× magnification with a Cossim U3CMOS14000 camera. A JSM-IT300 cold-field scanning electron microscope was used for examination of basidiospore ornamentation. At least 20 observation data were employed for each morphological character of every analysed collection. The format, $\alpha/\beta/\gamma$, represented the numbers of basidiospores,

basidiocarps and specimens that were measured microscopically. For those basidiospore dimensions, these were indicated as (*a*–) *b*–*c* (–*d*), the extremes of the measured values (*a* and *d*) are displayed in brackets. The values of *b* and *c* are 5th and 95th percentiles when observed readings were arranged from small to large. *Q* is the ratio of basidiospore length to width. The **Q** in bold is the mean value of *Q* plus or minus standard deviation. The pileipellis was vertically sectioned at the edge and centre of the pileus. Shapes and sizes of basidia, cystidia and hypha were observed, measured and illustrated. For other details on microscopic observation and measurement, see Li (2014) and Adamčík et al. (2019). Exsiccatae of these new species are preserved in the Macrofungus Section, Mycological Herbarium of Guizhou Academy of Sciences (HGAS-MF), Herbarium of Hebei Agricultural University (HBAU) and Herbarium of Fungi, Jiangxi Agricultural University (HFJAU).

DNA extraction, polymerase chain reaction (PCR) and sequencing

Tissue samples from dried specimens were ground in centrifuge tubes using abrasive rods attached to an electric drill. DNA extractions were performed using a modified CTAB method as in Li (2014). PCR reactions were carried out in a Dragonlab TC1000-G 96-well thermocycler. Sequences in the ITS region were amplified with primers ITS5 and ITS4 (White et al. 1990) using the reaction conditions of Li et al. (2019). PCR products were separated by electrophoresis on 1.2% agarose gels and stained with Biotium GelRed. The concentrations of extracted DNA and PCR products were determined by a ThermoFisher Scientific NanoDrop One spectrophotometer. Nucleotide concentration > 50 ng/μl was used as the criterion of a qualified PCR product for Sanger sequencing by GENEWIZ Inc. An ABI 3730XL DNA analyser and an Applied Biosystems Sanger sequencing kit were used following manufacturer's procedures by Biomed Gene Technology Company (Beijing, China).

Phylogenetic analyses

Bidirectional sequencing results were assembled with MegAlign in DNASTar LaserGene 7.1 (<https://www.dnastar.com>). Low quality nucleotide sites at both ends of the sequences were trimmed. All new sequences from this study were deposited in GenBank (<http://www.ncbi.nlm.nih.gov/nucleotide/>). The BLAST algorithm was used to search the similar sequences and for the new species. Table 1 contains closely matched ITS sequences of the new species (percent identities over 97%) retrieved from GenBank and UNITE (<https://unite.ut.ee/>) databases. Sampling for the phylogenetic backbone of *Russula* section *Ingratae* referred to Melera et al. (2017), Park et al. (2017) and Song et al. (2018). These sequences were combined with those of the new species and aligned in Mafft 7.428 with L-INS-I strategy applied (Nakamura et al. 2018). Five sequences from species of the other sections of *Russula* subgenus *Heterophyllidiae*, *R. cyanoxantha* (Schaeff.) Fr., *R. grisea* Fr., *R. heterophylla* (Fr.) Fr., *R. ilicis* Romagn. and *R. substriata* J. Wang et al., were chosen as out-group. The matrix file was manually optimised using BioEdit 7.0.5 (Hall 1999) and deposited in TreeBASE repository with study ID S28207 (<http://purl.org/phylo/treebase/phyloids/>

study/TB2:S28207?x-access-code=cda6b439c0eada24d5199bc264971fb5&format=html). Phylogenetic analyses were executed using Bayesian Inference (BI), Maximum Likelihood (ML) and Maximum Parsimony (MP) methods. Bayesian analysis was performed in MrBayes 3.2.7a (Ronquist et al. 2012). Best evolutionary model selection was carried out with MrModeltest 2.4 operated on PAUP* 4.0a165 through Akaike's Information Criteria (AIC) calculation (Nylander 2004). The calculation of posterior probabilities (PP) parameters was performed through the Markov chain Monte Carlo (MCMC) algorithm. The sampling frequency of the trees was set as every 100th generation. One cold and three hot Markov chains were run for 2×10^6 generations. The analysis ceased when the average standard deviation was maintained below 0.01. A percentage of 25% trees were discarded as burn-in before the construction of the 50% majority rule consensus tree. MP analysis was conducted in PAUP* 4.0a167 (Swofford 2004). The tree bisection-reconstruction (TBR) was carried out with a heuristic search. A total of 1000 replicates were set for bootstrap support (Felsenstein 1985). The setting of maxtrees was 5000. Branches collapsed when minimum length was zero. A Kishino-Hasegawa (KH) test (Kishino and Hasegawa 1989) was executed to determine whether trees were significantly different. The consistency index (CI), homoplasy index (HI), retention index (RI), rescaled consistency index (RC) and tree length (TL) were performed in MP analysis. ML analysis was performed in raxmlGUI 1.5b3 with 1000 replicates (Silvestro and Michalak 2012). Trees were displayed and exported in FigTree 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>). Names of species in Fig. 1 and Table 1 were cited from source databanks. Definitions for clades and complexes were also presented in Fig. 1.

Results

Phylogenetic analyses

A total of 112 ITS sequences (107 of sect. *Ingratae* and 5 of out-groups), including 13 newly-generated ones, were analysed in this study. The alignment for ITS phylogenetic analyses was composed of 543 characters including gaps. Of these characters in the matrix, 266 were variable, 201 were parsimony-informative, 65 variable characters were parsimony-uninformative. The parameters of MP analysis were CI 0.444, HI 0.784, RI 0.784, RC 0.348 and TL 869. The most suitable model for BI and MP analyses is GTR+I+G.

The resulting MP, ML and BI phylograms are consistent in topology of highly supported basal ranks (Clades A, B, C, D, E, F, H and I); thus, only the MP tree is presented in Fig. 1. A total of nine complexes and 24 species rank clades can be recognised with high support values. The 11 Chinese sequences were grouped in three clades that were further described as new species of *R. straminella*, *R. subpectinatoides* and *R. succinea*. High bootstraps and posterior probabilities supporting these clades are distinctly independent from those of other known taxa. Clades H, F and C in Fig. 1 generally corresponded with clades 1, 4 and 3 of Lee et al. (2017), in which species in Clade 2 are represented by Clades E and I in this study. The Indian and Chinese specimens of

Table 1. The species, specimens and GenBank accession numbers of ITS sequences analysed in this study.

| Species | Specimen No. | Origin | GenBank accession | Reference |
|----------------------------|-----------------------|------------------------------|-------------------|-------------------------|
| <i>Russula</i> aff. | MEL H4784 | Australia: Tasmania | EU019932 | Lebel and Tonkin (2007) |
| <i>pilosella</i> | | | | |
| <i>R. ahmadii</i> | LAH 35004 | Pakistan: Khyber Pakhtunkhwa | KT834638 | Jabeen et al. (2017) |
| | LAH 18081013 | Pakistan: Khyber Pakhtunkhwa | KU535609 | Jabeen et al. (2017) |
| | SB138 | Pakistan | HG796943 | Jabeen (2016) |
| <i>R. amerorecondita</i> | F PGA17-017 | USA: Indiana | MN130066 | Adamčík et al. (2019) |
| <i>R. ammophila</i> | MA-Fungi 51165 | Spain: Huelva | AJ438038 | Vidal et al. (2002) |
| <i>R. amoenolens</i> | TUB nl27.9.95.6 | Germany | AF418615 | Eberhardt (2002) |
| | MICH 12838 | France | KF245510 | – |
| <i>R. cf. amoenolens</i> | HMJAU37317 | China: Heilongjiang | KY357332 | Liu et al. (2017) |
| <i>R. aromatica</i> | PNW 5607 | USA: Oregon | AY239331 | – |
| <i>R. arunii</i> | CUH AM261 | India: West Bengal | KY450661 | Crous et al. (2017) |
| <i>R. brunneonigra</i> | DAR H5813 | Australia: New South Wales | EU019945 | Lebel and Tonkin (2007) |
| <i>R. catillus</i> | SFC 20120827-01 | Korea: Daehak-dong | KX574686 | Lee et al. (2017) |
| | SFC 20120919-35 | Korea: Daehak-dong | KX574688 | Lee et al. (2017) |
| | LHJ150915-19 | China: Guangdong | MK860690 | – |
| <i>R. cerolens</i> | OSC 76727 | USA: Oregon | KF245505 | – |
| | F 36 | USA: California | JN681168 | – |
| <i>R. cf. amoenolens</i> | MICH12838 | France | KF245510 | – |
| <i>R. cf. pulverulenta</i> | NYBG 4-1144IS79 | USA | AY061736 | Miller and Buyck (2002) |
| <i>R. cyanoxantha</i> | PC SM/BB 5 | Europe | AY061669 | Miller and Buyck (2002) |
| <i>R. echidna</i> | HO 593336 | Australia: Tasmania | MN130079 | Adamčík et al. (2019) |
| | HO 593337 | Australia: Tasmania | MN130080 | Adamčík et al. (2019) |
| <i>R. fluvialis</i> | KUO JR8666 | Finland: Savonia Borealis | MN130084 | Adamčík et al. (2019) |
| | KUO JR8313 | Finland: Northern Savonia | MN130085 | Adamčík et al. (2019) |
| | HMJAU 32234 | China: Heilongjiang | KX095018 | – |
| <i>R. foetens</i> | TUB hue124 | Germany | AF418613 | Eberhardt (2002) |
| | GENT FH-12-277 | Germany: Keula | KT934016 | Looney et al. (2016) |
| | HMJAU38004 | China: Heilongjiang | KY681438 | Liu et al. (2017) |
| <i>R. foetentoides</i> | LAH 04081023 | Pakistan: Khyber Pakhtunkhwa | HE647707 | Razaq et al. (2014) |
| | LAH 13081034 | Pakistan: Khyber Pakhtunkhwa | HE647708 | Razaq et al. (2014) |
| <i>R. foetentula</i> | 156 | USA: Tennessee | KJ834623 | Melera et al. (2017) |
| | 128 | Switzerland | KJ834574 | Melera et al. (2017) |
| <i>R. fragrantissima</i> | 98 | Italy | KJ530751 | Melera et al. (2017) |
| | 108 | Italy | KJ834596 | Melera et al. (2017) |
| <i>R. galbana</i> | BRIT13425 | Australia: Queensland | EU019936 | Lebel and Tonkin (2007) |
| <i>R. garyensis</i> | F PGA17-008 | USA: Indiana | MN130088 | Adamčík et al. (2019) |
| <i>R. gelatinosa</i> | K 16053119 | China: Guangdong | MH168574 | Song et al. (2018) |
| | K 15052626 | China: Guangdong | MH168575 | Song et al. (2018) |
| <i>R. granulata</i> | PC BB2004-226 | USA: Tennessee | EU598192 | – |
| | PC BB2004-225 | USA: Tennessee | EU598190 | – |
| | HMAS252604 | China: Jilin | KF850414 | Li (2014) |
| <i>R. grata</i> | E 00290534 | UK: Scotland | KF245532 | – |
| | TUB nl1348 | Germany | AF418614 | Eberhardt (2002) |
| | HMJAU38008 | China: Heilongjiang | KY681444 | Liu et al. (2017) |
| <i>R. grisea</i> | PC 2-1129IS75 | Europe | AY061679 | Miller and Buyck (2002) |
| <i>R. heterophylla</i> | PC 209RUF24 | Europe | AY061681 | Miller and Buyck (2002) |
| <i>R. hortensis</i> | IB 1997/0787 | Italy | HG798528 | – |
| <i>R. ilicis</i> | PC 563IC52 | Europe | AY061682 | Miller and Buyck (2002) |
| <i>R. illota</i> | MICH 73719 | France | KF245509 | – |
| | UE 26.07.2002-3 | Sweden | DQ422024 | Eberhardt (2002) |
| <i>R. inamoena</i> | 107 | Italy: Punta Chiappa | KJ834597 | Melera et al. (2016) |
| | 109 | Italy: Punta Chiappa | KJ834595 | Melera et al. (2016) |
| <i>R. indocatillus</i> | HGAS-MF 009917 | China: Guizhou | MN649191 | This study |
| | HGAS-MF 009903 | China: Guizhou | MN649192 | This study |
| <i>R. indocatillus</i> | AG 18-1653 | India: Uttarakhand | MN581165 | Ghosh et al. (2020) |
| <i>R. insignis</i> | HMAS 267740 | China: Heilongjiang | KF850404 | Li (2014) |
| | PC Buyck 00.2149 | Europe | AY061700 | Miller and Buyck (2002) |
| <i>R. mistiformis</i> | JC170305 | Spain: Castilla-Leon | MK105677 | Vidal et al. (2019) |
| | AMC H-69 | Spain: Castilla-Leon | MK105680 | Vidal et al. (2019) |

| Species | Specimen No. | Origin | GenBank accession | Reference |
|-----------------------------------|-----------------------|------------------------|-------------------|---------------------------|
| <i>R. mutabilis</i> | BHI-F384a | USA: Massachusetts | MF161239 | Haelewaters et al. (2018) |
| | DPL 10654 | USA: Texas | KF810137 | – |
| <i>R. neerimea</i> | MEL2101871 | Australia: Victoria | EU019915 | Lebel and Tonkin (2007) |
| <i>R. nondistincta</i> | OSC 62139 | USA: Oregon | KP859276 | – |
| <i>R. obscuricolor</i> | KD 16-30 | India: Sikkim | MF805816 | Das et al. (2017) |
| | KD 16-22 | India: Sikkim | MF805817 | Das et al. (2017) |
| <i>R. oleifera</i> | TU 116011 | Benin | UDB016936 | – |
| | TU 102082 | Zambia | UDB013811 | – |
| <i>R. ombrophila</i> | 86 | Spain | KF971694 | Melera et al. (2016) |
| <i>R. parkii</i> | Trappe 14997 | USA | AY239335 | – |
| <i>R. pectinata</i> | PC Buyck 2304 | Europe | AY061706 | Miller and Buyck (2002) |
| | 2010BT02 | Germany | KF318081 | Melera et al. (2016) |
| | 2010BT48 | Germany | KF318082 | Melera et al. (2016) |
| <i>R. pectinatoides</i> | MICH 52692 | USA: Tennessee | KF245518 | – |
| | HMAS251202 | China: Yunnan | JX425405 | Li (2014) |
| | NYS2303.1 | USA: New York | KU640189 | Melera et al. (2016) |
| <i>R. pila</i> | MA-Fungi 30667 | Spain | AF230893 | Calonge and Martín (2000) |
| <i>R. pilosella</i> | BRI-H5974 | Australia: Queensland | EU019941 | Lebel and Tonkin (2007) |
| <i>R. praetervisa</i> | UE 2006-11-12-01 | Italy | UDB019333 | – |
| | IB 1997-0812 | Italy | UDB019331 | – |
| <i>R. pseudocatillus</i> | GDGM 75338 | China: Guangdong | MK049974 | Yuan et al. (2019) |
| | K 15060706 | China: Guangdong | MK049975 | Yuan et al. (2019) |
| <i>R. pseudopectinatoides</i> | HMAS 265020 | China: Xizang | KM269079 | Li et al. (2015b) |
| | HMAS 251523 | China: Xizang | KM269077 | Li et al. (2015b) |
| <i>R. pulverulenta</i> | PC BB2004-245 | USA: Tennessee | EU598186 | – |
| <i>R. punctipes</i> | K 17052318 | China: Guangdong | MH168576 | Yuan et al. (2019) |
| | K 16051001 | China: Guangdong | MH168577 | Yuan et al. (2019) |
| <i>R. putida</i> | IB 1997/0791 | Italy | HG798527 | – |
| <i>R. recondita</i> | UPS AT2001049 | Sweden | DQ422026 | Eberhardt (2002) |
| | WGS 84 | Switzerland | KJ530750 | Melera et al. (2016) |
| | TU106223 | Estonia: Saare maakond | UDB011156 | – |
| <i>R. rufobasalis</i> | H15060622 | China: Guangdong | MH168567 | Song et al. (2018) |
| | H17052204 | China: Guangdong | MH168570 | Song et al. (2018) |
| <i>R. senecis</i> | SFC 20110921-18 | Korea: Socho-myeon | KX574698 | Lee et al. (2017) |
| | CUH AM102 | India: West Bengal | KP142981 | Khatua et al. (2015) |
| <i>R. shafferi</i> | OSC 51046 | USA: Washington | AY239327 | – |
| <i>R. similis</i> | OSC 44426 | USA: California | AY239329 | – |
| | Trappe 7753 | USA: Oregon | AY239349 | – |
| <i>Russula</i> sp. | LHJ170913-01 | China: Guangdong | MK860691 | Song et al. (2020) |
| <i>R. straminella</i> | HGAS-MF 009920 | China: Guizhou | MN649194 | This study |
| | HGAS-MF 009922 | China: Guizhou | MN649195 | This study |
| | HGAS-MF 009925 | China: Guizhou | MN649189 | This study |
| <i>R. subfoetens</i> | HMJAU38006 | China: Heilongjiang | KY681430 | Liu et al. (2017) |
| | TU101908 | Finland: Nilsia | UDB016206 | – |
| <i>R. subfulva</i> | Trappe 14998 | USA: Oregon | AY239321 | – |
| <i>R. subpectinatoides</i> | HBAU15023 | China: Jiangsu | MW041163 | This study |
| | HBAU15024 | China: Jiangsu | MW041164 | This study |
| | HBAU15025 | China: Jiangsu | MW041165 | This study |
| | HBAU15026 | China: Jiangsu | MW041166 | This study |
| <i>R. subpunctipes</i> | RITF 2616 | China: Guangdong | MK860692 | Song et al. (2020) |
| | RITF 2617 | China: Guangdong | MK860693 | Song et al. (2020) |
| <i>R. substriata</i> | HKAS 102278 | China: Yunnan | MH724921 | Wang et al. (2019) |
| <i>R. succinea</i> | HGAS-MF 009909 | China: Guizhou | MN649196 | This study |
| | HGAS-MF 009904 | China: Guizhou | MN649188 | This study |
| | HGAS-MF 009906 | China: Guizhou | MN649198 | This study |
| | HGAS-MF 009915 | China: Guizhou | MN649190 | This study |
| <i>R. succinea</i> | HFJAU0301 | China: Jiangxi | MN258682 | – |
| <i>R. ventricosipes</i> | PC 0142480 | USA | KY800364 | Buyck et al. (2017) |
| <i>R. vinaceocuticulata</i> | PDD 64246 | New Zealand | GU222258 | – |

Note: Species, specimens and GenBank accession numbers in bold are newly collected and sequenced in this study.

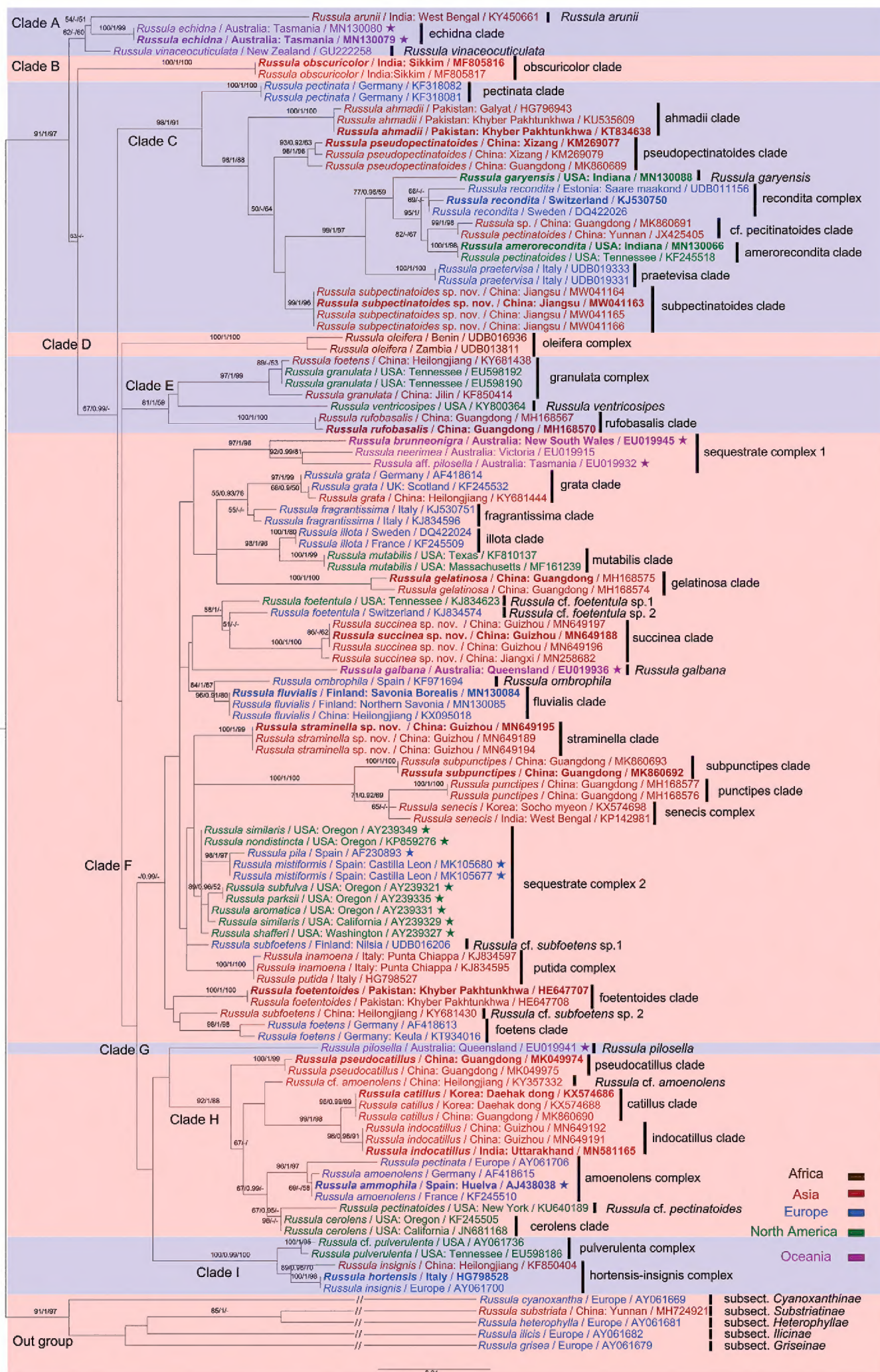


Figure 1. Phylogenetic tree generated from Bayesian analysis of ITS sequences. Main clades corresponding to subsections of sect. *Ingratae* are indicated in colour blocks. Holotypes of the new species are shown in bold. Values of posterior probabilities (PP) of MrBayes (≥ 0.9) and bootstraps of ML and MP analyses (≥ 50) are presented above the nodes as (MLBS/PP/MPBS).

R. indocatillus clustered together and formed a strongly supported, distinct clade (MLBS 96, PP 0.99, MPBS 89). The new species, *R. straminella*, formed an independent lineage in Clade F. The concrete phylogenetic status of *R. straminella* still remains unsolved in ITS sequence analyses. The new species *R. succinea* and two North American specimens were identified as *R. foetentula* with passable support (MPBS 58, PP 1). The new species, *R. subpectinatoides*, clustered with a majority of members from clade C and formed a highly supported clade (MLBS 96, PP 1, MPBS 88). The close relationship with *R. pseudopectinatoides* indicated in similarity searching was not supported in phylogenetic topologies.

The DNA sequence similarity search results for the ITS1–5.8S–ITS2 region of the new species are as follows: two North American specimens of gasteroid *R. similis* Trappe & T.F. Elliott (AY239349 and KC152107) had the highest sequence identity (98.2%) to the new species *R. straminella*, then *R. nondistincta* Trappe & Castellano (KP859276) (98.1%); *R. pseudopectinatoides* (KM269079) had the highest sequence similarity (98%) to the new species *R. subpectinatoides*, then *R. praetervisa* Sarnari (95%); *R. foetentula* Peck (KJ834623) had the highest sequence identity (96.9%) to the new species *R. succinea*, then *R. subfoetens* W.G. Sm. (UDB016206) (94%). The Chinese collections of *R. indocatillus* had sequence identities of 99% to its type specimens (MN581483 and MN581165) from India.

Taxonomy

***Russula indocatillus* A. Ghosh, K. Das & R.P. Bhatt, Nova Hedwigia 111(1–2): 124. 2020.**

Figs 2a, 3a, 4 and 5.

Basidiomata small to medium sized. Pileus 35–46 mm in diam., hemispherical when young, then plano-convex to applanate, depressed at centre when mature, rarely infundibuliform, viscid when wet, brownish tinged, intermixed with greyish-yellow fringe, Verona Brown (XXIX13"k), Chocolate (XXVIII7"m), to Cinnamon Brown (XV15'k) at centre, sometimes with a tinge of Argus Brown (III13m) or Brussels Brown (III15m), Pecan Brown (XXVIII13'i) or Hazel (XIV11"k) when old and dry; margin acute, slightly incurved first, straight when mature, slightly undulate, often cracked, tuberculate-striate 10–15 mm from the edge inwards, peeling 1/5–1/4 towards the centre, Ochraceous Tawny (XV15'i), Mikado Brown (XXIX13'i) or Tawny Olive (XXIX17'i) when young, often Avellaneous (XL17"b), Cinnamon (XXXI15") to Clay Colour (XXIX17") when mature. *Lamellae* adnate, rarely sub-free, 2–5 mm in height at mid-radius of pileus, fragile, rarely forked near the stipe, interveined, pale cream tinged, White (LIII) when young, Cream Colour (XVI19'f) in age, often stained yellowish to brownish with Buckthorn Brown (XV17'i) to Yellow Ochre (XV17'); edge even, narrowing towards the pileus margin, 9–16 per cm near the pileus margin; lamellulae rare. *Stipe* subcentral to central, 2.5–4.7 × 1–1.4 cm, cylindrical to subclavate, rarely tapered towards the base, annulus absent, first smooth, then often longitudinally rugulose in age, White (LIII), rarely stained with brownish tinge of

Aniline Yellow (IV19i) to Honey Yellow (XXX19"), first stuffed, hollow when mature. *Context* 2–4 mm thick at the centre of pileus, initially White (LIII), Light Ochraceous-Salmon (XV13'd) to Primuline Yellow (XVI19') when mature, unchanging or slowly turning Ochraceous-Tawny (XV15') to Buckthorn Brown (XV17'i) when injured or touched, brittle; taste mild, rarely slightly acrid when young; odour indistinct. *Spore print* cream-coloured (Romagnesi IIc–IIId).

Basidiospores [200/8/4] (4.9–) 5.3–6.8 (–7.3) \times (4.7–) 5.0–5.9 (–6.3) μm , $Q = (1.01\text{--}) 1.05\text{--}1.28\text{ (–}1.33\text{)}$ ($Q = 1.18 \pm 0.08$), $6.1 \times 5.5 \mu\text{m}$ in average, subglobose to broad ellipsoid, ornamentation composed of conical to verrucous amyloid warts of very different sizes, mostly isolated, rarely linked as short ridges or with occasional line connections, not reticulate, warts 0.7–1 μm in height; suprahilar spot inamyloid and indistinct. Basidia 27–39 \times 8–9 μm , hyaline in KOH, clavate to subclavate, four-spored, projecting 15–20 μm beyond the hymenium; sterigmata 3–6 μm , pointed, often straight, slightly tortuous towards the tip. Hymenial cystidia rare, less than 200/mm², 56–70 \times 6–9 μm , fusiform to subclavate, rarely subcylindrical, thin-walled, projecting 20–40 μm beyond the hymenium, apex often mucronate, contents sparse, unevenly distributed, granular, greyish in SV. Pileipellis two layered, composed of suprapellis (80–150 μm thick) and subpellis (100–150 μm thick). Suprapellis an ixotrichoderm at pileus centre, composed of oblique to erect, septate, hyaline hyphae; acid-resistant encrustations absent, terminal cells cylindrical to subcylindrical, apex obtuse, rarely mucronate, mostly 40–70 μm in length; pileus margin a trichoderm composed of repent to tilted elements, terminal cells mostly 7–20 (–25) μm in length, ampullaceous, ellipsoid or cylindrical, obtuse to mucronate at apex, longer terminal cells similar to those in pileus centre also present; subapical cells contain islands of more or less inflated, 2–4 septate cells. Pileocystidia present in suprapellis and subpellis, abundant at pileus centre, dispersed at margin, one-celled, subulate, lageniform, fusiform, cylindrical, rarely appendiculate, 4–6 μm in width, many in suprapellis 15–25 μm in length, others up to 60 μm , even reaching a length of 100 μm in subpellis, apex mucronate, acicular to lanceolate in suprapellis, obtuse in subpellis, contents granulate, sparse, greyish in SV. Subpellis composed of repent to irregularly interlaced, inflated, septate hyphae 3–5 μm wide. Clamp connections absent in all tissues.

Specimens examined. China, Guizhou Province, Weining Yi, Hui, and Miao Autonomous County, Caohai National Nature Reserve, 26°53'N, 104°12'E, alt. 2171 m, on the ground in coniferous forest, 9 September 2017, C.Y. Deng A (HGAS-MF 009903); *ibid*, alt. 1987 m, C.Y. Deng dcy2306 (HGAS-MF 009918); *ibid*, alt. 2053 m, C.Y. Deng dcy2303 (HGAS-MF 009911); *ibid*, alt. 2106 m, C.Y. Deng CH2017090971 (HGAS-MF 009917).

Habit and habitat. Single to scattered on yellow brown soil in coniferous forest dominated by *Pinus armandii* and *P. yunnanensis* at 1900–2200 m altitude.

Distribution. China (Guizhou) and India (Uttarakhand).

Notes. The Chinese collections fit well with the original description of Ghosh et al. (2020), except for a few differences. The Indian specimens have longer basidia, 35–60 \times 9–11 μm . The original description of *R. indocatillus* also noted that the type

specimen was collected in a temperate mixed forest with *Myrica*, *Quercus* and *Rhododendron*. The coniferous tree species in this habitat were not mentioned. The Chinese collection is from a subalpine coniferous forest of subtropical region dominated by *Pinus* spp. with the main undergrowth species of *Berberis cavaleriei*, *Corylus yunnanensis*, *Elaeagnus umbellata* and *Rosa sweginzowii* (He et al. 2019).

Amongst the closely-related species in Clade H, *R. amoenolens* Romagn. and *R. cerolens* Shaffer have a strongly acrid taste, disagreeable sub-spermatocytic odour, basidiospore length up to 9 μm and longer hymenial cystidia up to 100 μm (Shaffer 1972; Romagnesi 1985; Sarnari 1998); *R. catillus* lacks lamellulae, has longer basidia $42\text{--}49 \times 9.3\text{--}11.7 \mu\text{m}$, shorter pileipellis terminal cells $41\text{--}72 \times 3\text{--}7 \mu\text{m}$ and lacks pileocystidia (Lee et al. 2017); *R. pseudocatillus* has larger basidiospores $7\text{--}9.2 \times 5.1\text{--}6.7 \mu\text{m}$ with higher ornamentation (up to 1.2 μm) which is never reticulate (Yuan et al. 2019).

Some members of *R. sect. Ingratae*, which were originally described from Himalayan Mountains and adjacent south-western China, may be confused with *R. indocatillus* in the field. Their main morphological differences are as follows: *R. abbotensis* has a crustose to areolate pileus with purplish-red to reddish-brown tinges, an ixotrichoderm pileipellis with pileocystidia 5 μm in width and an occurring in ectomycorrhizal association with *Quercus* spp. (Das and Sharma 2005); *R. arunii* can be distinguished by its fishy odour, amyloid suprahilar spot, 3–4 μm wide pileocystidia, mostly with a capitate apex and habitat in a tropical rain forest of *Pterygota alata* (Crous et al. 2017); *R. ahmadii* has larger basidiospores $(5.6\text{--}) 6.1\text{--}9.2\text{--}(9.4) \times (5\text{--}) 5.1\text{--}6\text{--}(6.5) \mu\text{m}$ with low (up to 0.3 μm high), partly reticulated ornamentation and cutis type of pileipellis (Jabeen et al. 2017); *R. foetentoides* can be distinguished from *R. indocatillus* by its smooth pileus margin, absence of lamellulae and its basidiospore ornamentation of 1.7–2 μm in height (Razaq et al. 2014); *R. natarajanii* differs in having larger basidiospores, $6.8\text{--}8.8 \times 5.8\text{--}7.1 \mu\text{m}$ and longer hymenial cystidia, $60\text{--}90 \times 6\text{--}10.5 \mu\text{m}$ (Das et al. 2006); *R. pseudopectinatoides* has larger basidiospores $(6\text{--}) 6.5\text{--}9\text{--}(9.5) \times (5\text{--}) 5.1\text{--}6\text{--}(6.5) \mu\text{m}$ with partly reticulate ornamentation, longer hymenial cystidia up to 90 μm and terminal cells of suprapellis hyphae often with obtuse to ventricose apex (Li et al. 2015b); *R. succinea* differs in larger basidiospores with incompletely reticulated ornamentations, longer basidia and pileocystidia up to 10 μm in width (Figs 10 and 11); *R. tsokae* can be distinguished from *R. indocatillus* by its larger basidiomata 8–13 cm in diam., yellowish-orange tinged stipe and larger basidiospores $6.8\text{--}8.8 \times 5.8\text{--}7.1 \mu\text{m}$ with reticulated ornamentation up to 2 μm high (Das et al. 2010).

***Russula straminella* G.J. Li & C.Y. Deng, sp. nov.**

Figs 2b, 3b, 6 and 7.

Fungal Names: FN 570758

Etymology. referring to the yellowish tinged pileus

Holotype. China, Guizhou Province, Guiyang City, Yunyan District, Guizhou Botany Garden, 26°37'N, 106°43'E, alt. 1107 m, on the ground in coniferous forest,



Figure 2. Basidiomata **A** *Russula indocatillus* **B** *R. straminella* **C–D** *R. subpectinatoides* **E–F** *R. succinea*. Bars: 10 mm.

8 July 2017, C.Y. Deng 2017–209 (HGAS-MF 009922, **Holotype**). GenBank accession: MN649195 (ITS).

Diagnosis. This species is characterized by the yellow, brownish-yellow to brown pileus, tuberculate-striate margin, adnate lamellae tinged ochraceous when bruised, rare lamellulae, white stipe turning brownish-yellow when injured, mild to rarely acrid context, cream spore print, globose, subglobose to broad ellipsoid basidiospores $(5.4\text{--}) 5.8\text{--}7.1\text{--}(7.6) \times (4.7\text{--}) 5.1\text{--}6.5\text{ }\mu\text{m}$, $6.4 \times 5.6\text{ }\mu\text{m}$ on average, with verrucous to conical, partly reticulate ornamentations $0.7\text{--}1\text{ }\mu\text{m}$ in height, subclavate to clavate basidia $33\text{--}40 \times 9\text{--}11\text{ }\mu\text{m}$, clavate to subclavate hymenial cystidia $56\text{--}70 \times 8\text{--}10\text{ }\mu\text{m}$, a suprapellis composed of two layers, a trichoepithelium at pileus centre and an ixotrichoderm towards the margin, pileocystidia abundant at pileus centre, but sparse in margin, a cutis type of subpellis and habitat on the ground in coniferous forests.

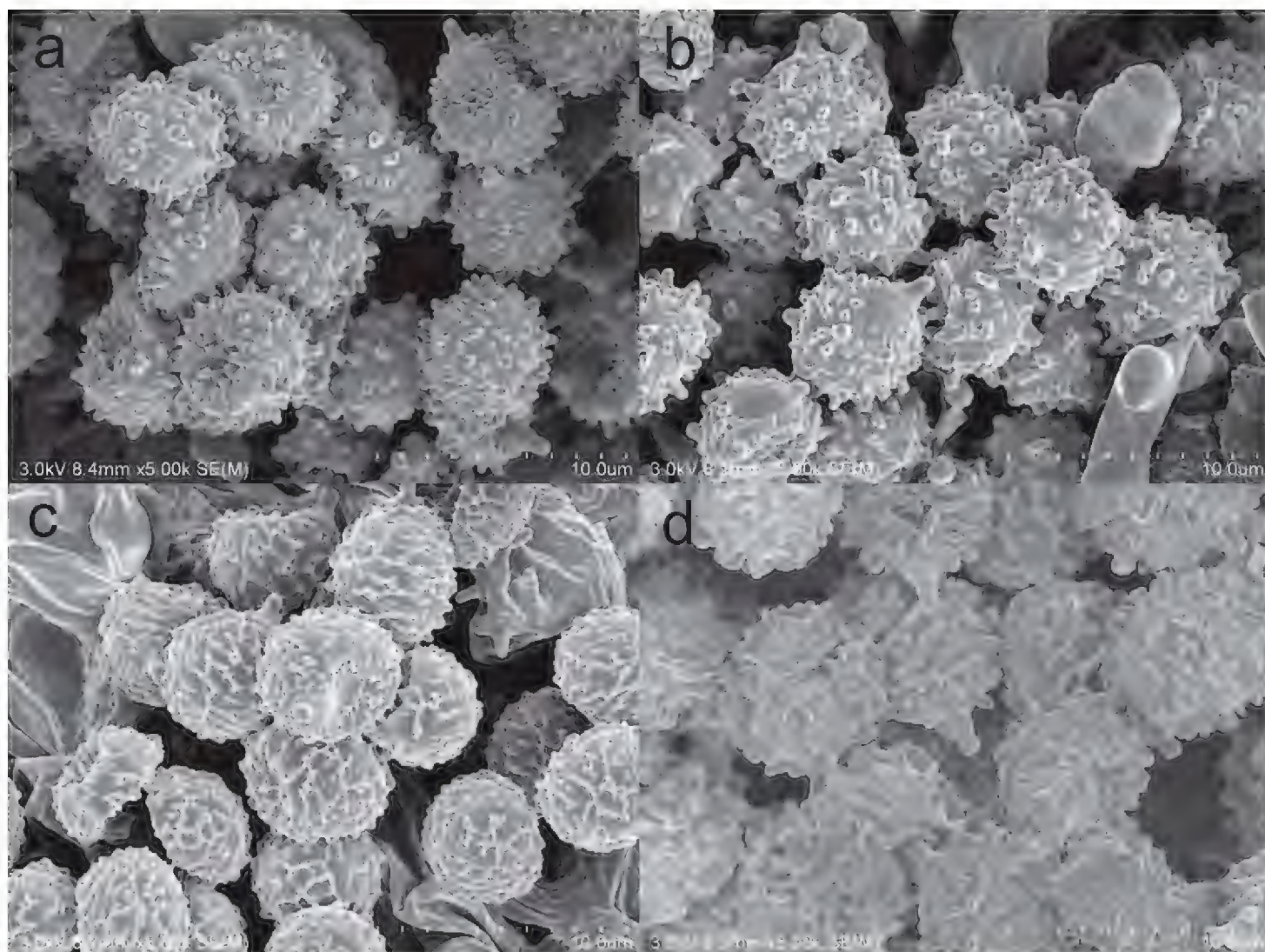


Figure 3. SEM photo of basidiospores **A** *Russula indocatillus* **B** *R. straminella* **C** *R. subpectinatoides* **D** *R. succinea*.

Description. *Basidiomata* small to medium sized. Pileus 33–57 mm in diam., initially flat to hemispherical, then plano-convex to applanate, finally often concave at centre, gelatinised, yellowish to brownish-yellow tinged, intermixed with brownish fringe, Argus Brown (III13m), Warm Sepia (XXIX13"m), to Verona Brown (XXIX13"k) at centre, rarely with a paler tinge of Mikado Brown (XXIX13"i), Rood's Brown (XXVIII11"k) to Cacao Brown (XXVIII9"i); margin acute to subacute, enrolled when young, often undulate, sometimes cracked when mature, tuberculate-striate 8–15 mm from the edge inwards, peeling 1/5–1/4 towards the centre, first Aniline Yellow (IV19i), Sayal Brown (XXIX15") to Cinnamon Buff (XXIX15"d), finally Mikado Brown (XXIX13"i), Snuff Brown (XXIX15"k) to Clay Colour (XXIX17"). *Lamel-lae* adnate, fragile, occasionally forked near the stipe and pileus margin, interveined, first White (LIII), then of Cream Colour (XVI19'f) when mature, often having an ochraceous tinge of Olive Ochre (XXX21"), Isabella Colour (XXX19"i) to Honey Yellow (XXX19") when bruised, taste mild to slightly acrid; edge even, narrowing towards the pileus edge, 8–16 pieces per cm in the edge; lamellulae rare. *Stipe* central, 3.5–6.5 × 1–1.5 cm, cylindrical, slightly tapering towards the base, annulus absent, first smooth, slightly longitudinally rugulose when mature, White (LIII) when young, turning a pale brownish-yellow tinge of Kaiser Brown (XIV9'k), Aniline Yellow (IV19i)

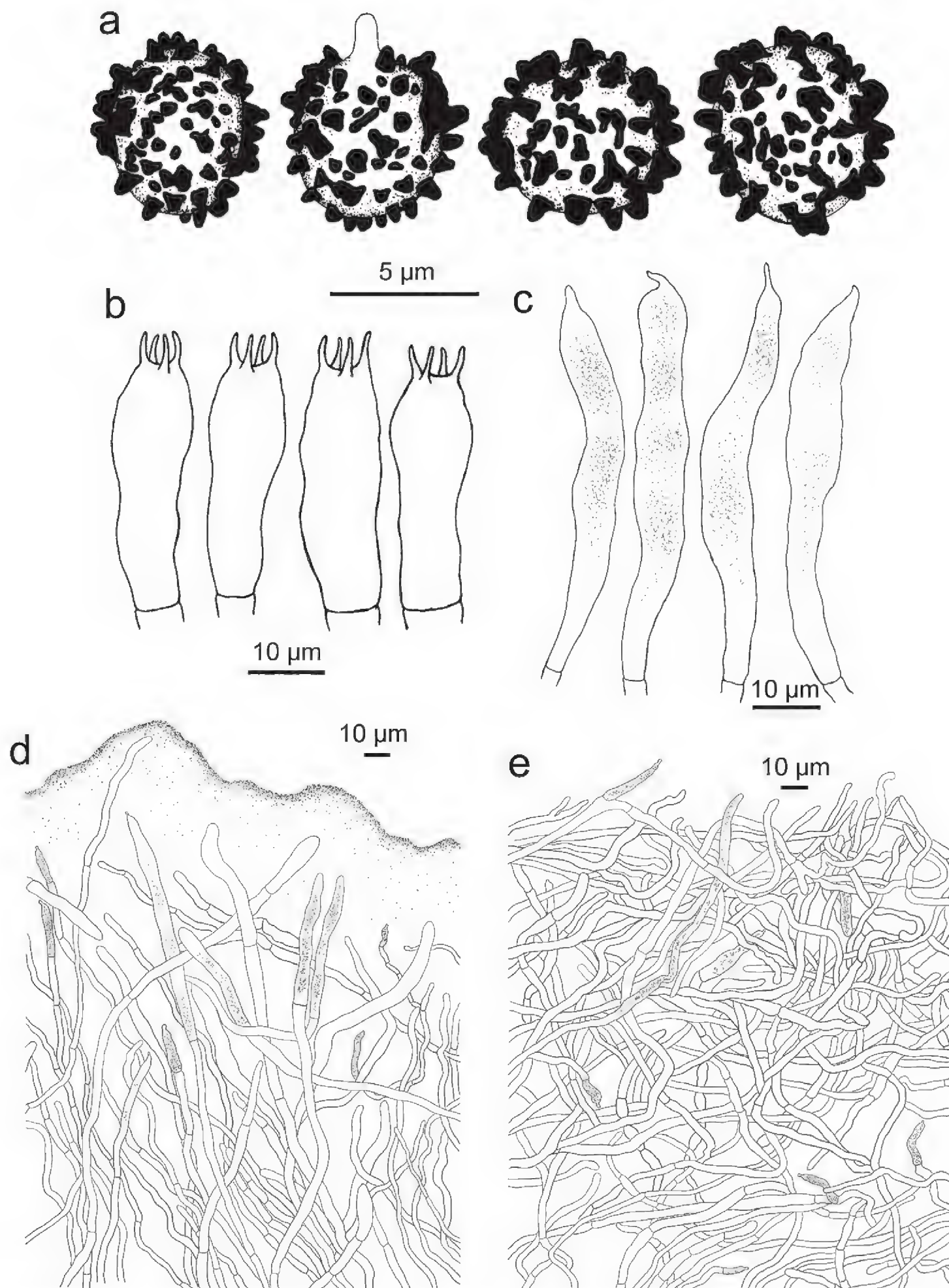


Figure 4. *Russula indocatillus*, holotype **A** basidiospores **B** basidia **C** hymenial cystidia **D** suprapellis in pileus centre **E** suprapellis in pileus margin.

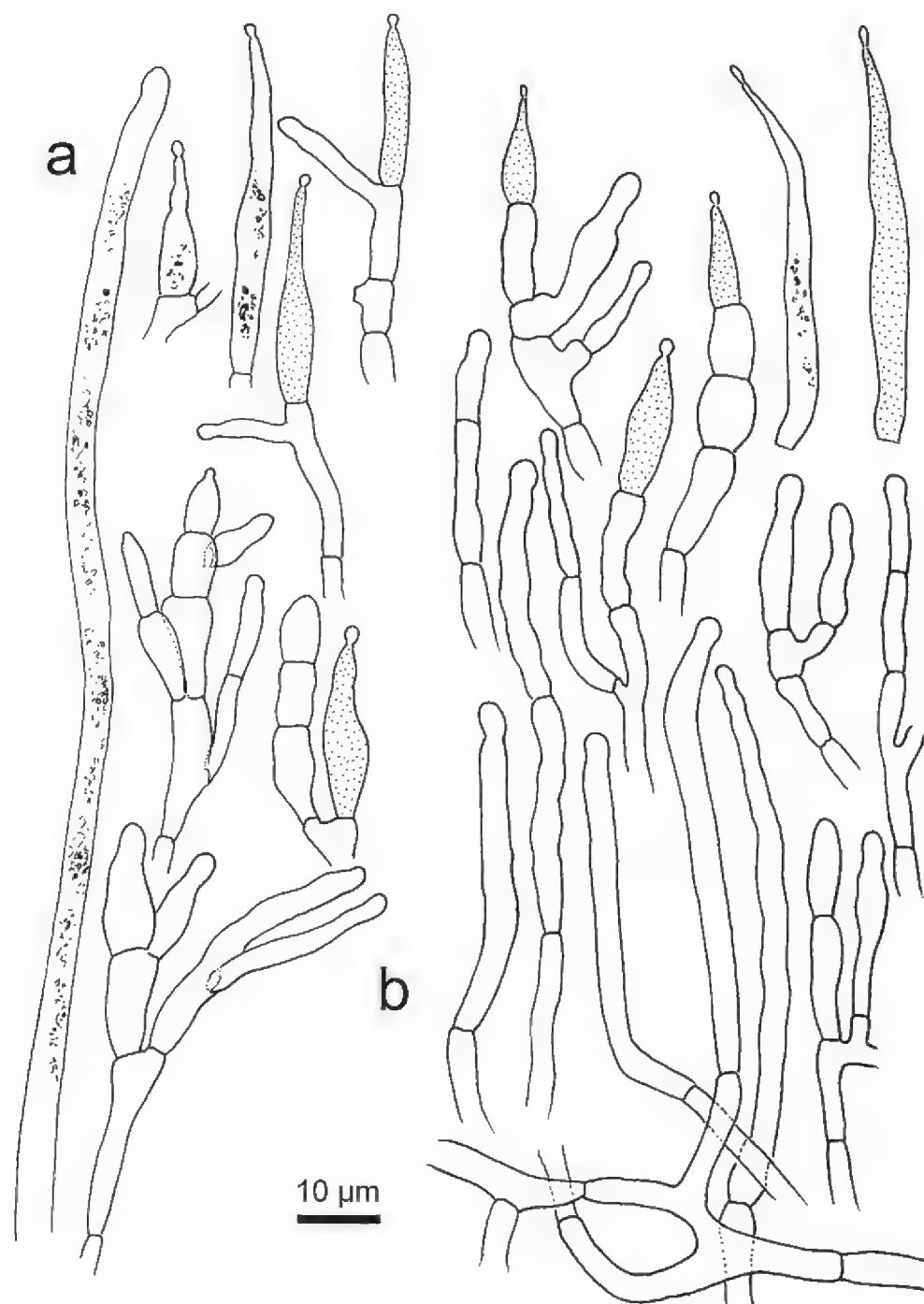


Figure 5. *Russula indocatillus*, holotype **A** hyphal extremities in pileipellis margin **B** hyphal extremities in pileus centre.

to Buckthorn Brown (XV17'i) after bruising, initially stuffed, fistulous to hollow when mature. *Context* White first, slowly turning a pale ochraceous tinged of Yellow Ochre (XV17') to Ochraceous-Buff (XV15'b) when injured, 2–4 mm thick at the centre of pileus, compact; taste mild, rarely slightly acrid, with no distinct odour. *Spore print* cream coloured (Romagnesi IIc–IIId).

Basidiospores [150/6/3] (5.4–) 5.8–7.1 (–7.6) \times (4.7–) 5.1–6.5 μm , $Q = (1.00\text{--}) 1.03\text{--}1.28$ (–1.31) ($Q = 1.15 \pm 0.07$), $6.4 \times 5.6 \mu\text{m}$ in average, globose, subglobose to broadly ellipsoid, rarely ellipsoid, ornamentation amyloid, composed of verrucous to conical warts 0.7–1 μm in height, often linked by fine lines as short ridges, partly reticulate, rarely isolated; suprahilar area inamyloid, but distinct. *Basidia* 33–40 \times

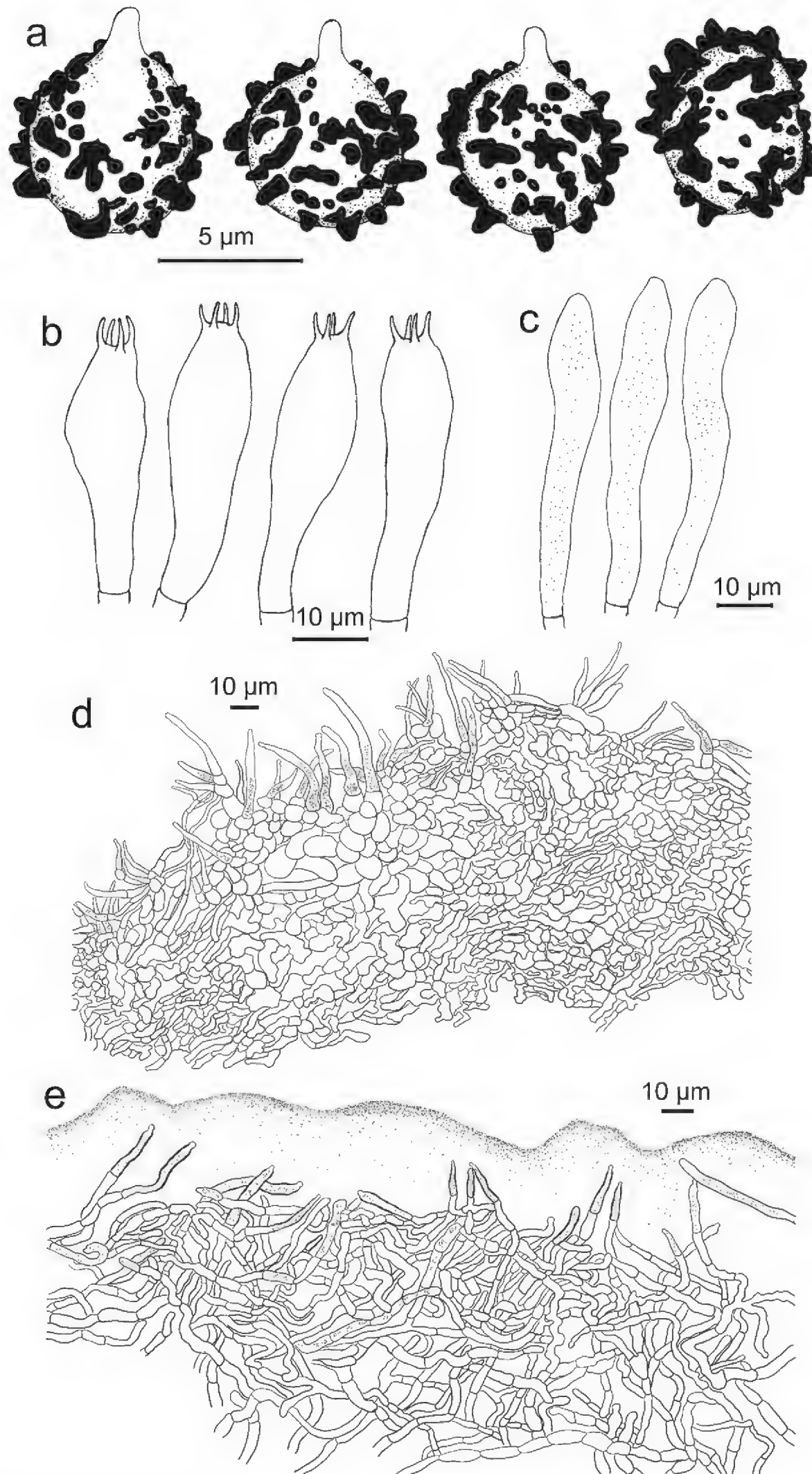


Figure 6. *Russula straminella*, holotype **A** basidiospores **B** basidia **C** hymenial cystidia **D** suprapellis and partial subpellis in pileus centre **E** suprapellis in pileus margin.

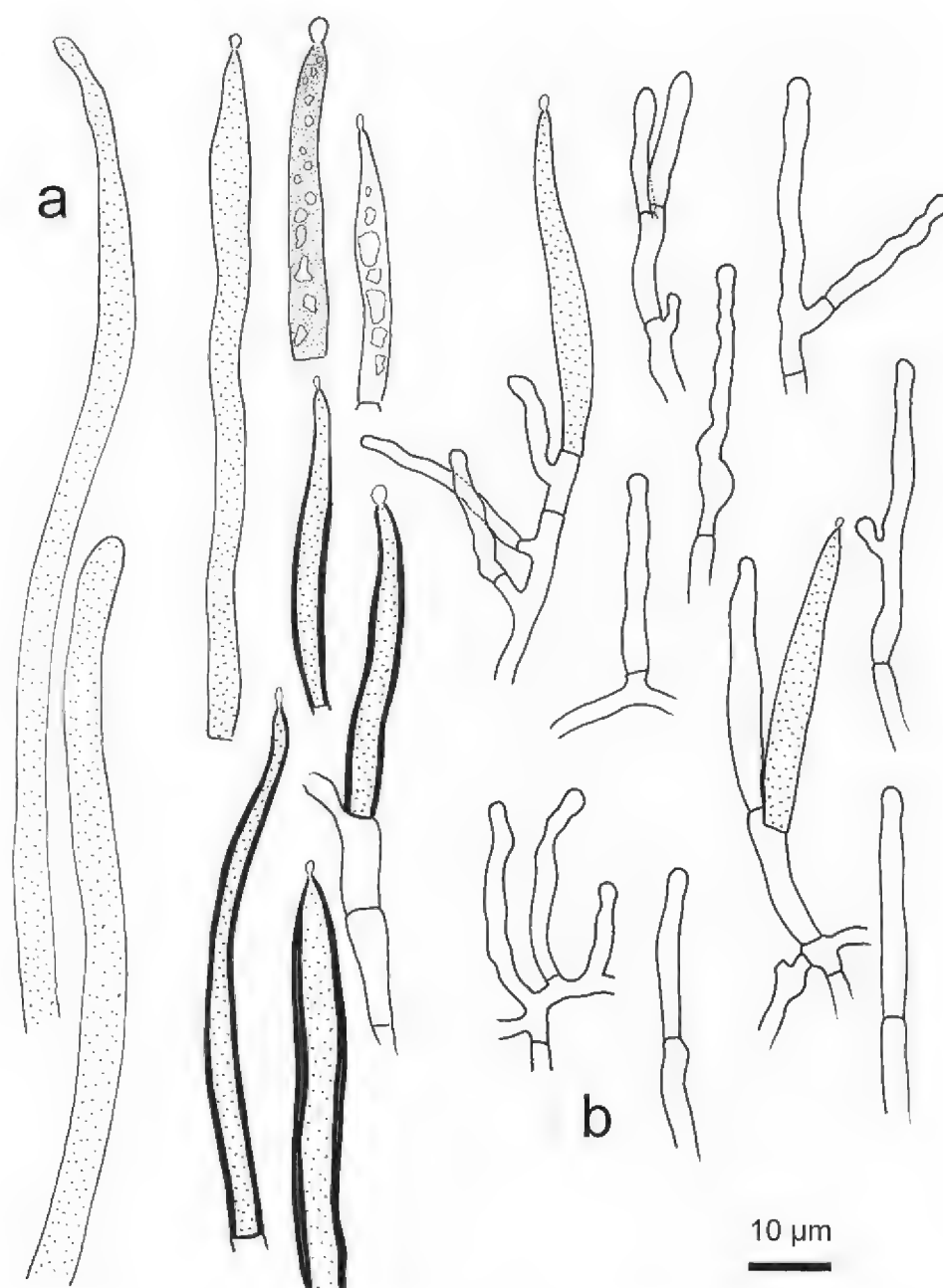


Figure 7. *Russula straminella*, holotype **A** hyphal ends in pileipellis margin **B** hyphal ends in pileus centre.

9–11 μm , hyaline, often yellowish in KOH, subclavate to clavate, sometimes cylindrical, mostly with four sterigmata 4–7 μm long. *Hymenial cystidia* rare, less than 500/mm², 56–70 \times 8–10 μm , clavate to subclavate, rarely subfusiform, projecting 20–40 μm beyond hymenium, apex rounded, contents sparse, granular, evenly distributed, pale greyish in SV. *Pileipellis* two-layered, clearly distinguished from the subjacent sphaerocytes. *Suprapellis* 70–130 μm thick, acid-resistant encrustations absent, a trichoepithelium at pileus centre, partly an ixo-trichoepithelium, composed of erect to suberect hyphae, terminal cells cylindrical, 20–40 \times 3–5 μm , obtuse at apex, partly ventricose, subapical cells sometimes inflated, rarely branched, 15–25 \times 8–12 μm , an ixotrichoderm at pileus margin, composed of erect to ascending, rarely repent hyphae, terminal cells 30–55 \times 3–5 μm , cylindrical, often thick-walled, tapered to mucronate at apex. *Pileocystidia* abundant, often fasciculate at pileus centre, narrowly lanceolate to bayonet-shaped, 30–60 \times 5–8 μm , one-celled, contents granular, blackish-grey in SV. *Pileocystidia* sparse at the pileus margin, cylindrical, 4–8 μm in width, slightly tapered at apex, contents grey in SV. *Subpellis* composed of

loosely interwoven, mostly repent, septate hyphae often inflated, 3–8 μm in width. *Clamp connections* absent in all tissues.

Additional specimens examined. China, Guizhou Province, Guiyang City, Yunnan District, Guizhou Botany Garden, 26°37'N, 106°43'E, alt. 1074 m, on the ground in coniferous forest, 8 July 2017, C.Y. Deng dcy2305 (HGAS-MF 009920, paratype); *ibid.*, alt. 1385 m, C.Y. Deng dcy2302 (HGAS-MF 009925, paratype).

Habit and habitat. Single to scattered on yellow brown soil in coniferous forest dominated by *Pinus armandii* and *P. massoniana* at 1100–1400 m altitude.

Distribution. China (Guizhou).

Notes. This new species can be distinguished from members of *R.* sect. *Ingratae* described from China and the Himalayan region as follows: *Russula gelatinosa*, *R. guangdongensis* Z.S. Bi & T.H. Li, *R. punctipes*, *R. senecis*, *R. subpunctipes* and *R. tsokae* have basidiospore ornamentation composed of high wings (often above 2 μm), ranging over long distances or even encircling (Bi and Li 1986; Song et al. 2018, 2020). The Asian species of *R.* sect. *Ingratae*, *R. abmadii*, *R. natarajanii* and *R. pseudopectinatoides* have basidiospore ornamentation lower than 0.7 μm (Das et al. 2006; Li et al. 2015b; Jabeen et al. 2017). For species that have similar basidiospore ornamentation, *R. abbotensis* has reddish-brown to purplish-red tinges on pileus surface, pruinose to scurfy stipe at base, larger basidiospores, 8–10 \times 7.3–8.5 μm and hymenial cystidia with mucronate apices (Das and Sharma 2005); *R. arunii* has pileus turning light orange to greyish-orange when old, context having a fishy odour and narrow pileocystidia 3–4 μm in width (Crous et al. 2017); *R. indocatillus* has hymenial cystidia with mucronate, capitate, moniliform, rostrate or appendiculate apex with cylindrical or slightly inflated subapical cells (Ghosh et al. 2020); *R. obscuricolor* has a pale yellowish-white tinge in pileus margin, pungent and bitterish context, narrow pileocystidia 3–5 μm in width (Das et al. 2017); *R. pseudocatillus* has greyish-brown pileus centre, towards the margin very pale yellow, larger basidiospores, 7–9 μm in diam. and narrower pileocystidia (3–6 μm in width) unchanging in SV (Yuan et al. 2019); *R. rufobasalis* has reddish stipe base, mucronate or appendiculate apex of hymenial cystidia and thick-walled terminal cells (Song et al. 2018).

***Russula subpectinatoides* G.J. Li & Q.B. Sun, sp. nov.**

Figs 2c, 2d, 3c, 8 and 9.

Fungal Names: FN 570759

Etymology. named for its morphological resemblance to *R. pectinatoides* Peck.

Holotype. China, Jiangsu Province, Nanjing City, Qixia District, Nanjing Normal University, 32°06'N, 118°54'E, alt. 84 m, on the ground in coniferous forest, 28 August 2018, Q.B. Sun 2018001 (HBAU15030, **Holotype**). GenBank accession: MW1041163 (ITS).

Diagnosis. This species is characterised by the greyish-brown to brownish-yellow pileus, striate margin, adnate to subadnate lamellae rarely staining reddish-brown when bruised, infrequent lamellulae, context slowly turning pale ochre after injury and

slightly to moderately acrid taste, cream spore print, subglobose to broadly ellipsoid basidiospores $(5.3-5.6-6.3-7 (-7.3) \times (4.1-4.6-5.2-6 (-6.3) \mu\text{m})$, ornamentation $0.3-0.5 \mu\text{m}$ in height, composed of long ridges forming an incomplete to complete reticulum, fusiform to subclavate, basidia $27-50 \times 8-12 \mu\text{m}$, fusiform to subclavate hymenial cystidia $56-73 \times 6-12 \mu\text{m}$, pileipellis with one-celled, slender, mucronate, conical, needle-shaped to cylindrical pileocystidia, $5-7 \mu\text{m}$ in width; and habitat in coniferous forest.

Description. *Basidiomata* small to medium-sized. *Pileus* 18–95 mm in diam., initially hemispherical, concave at centre, turning applanate with age, often depressed at stipe, slightly viscous when young or humid, greyish-brown to brownish-yellow tinged, intermixed with dark brown fringe, Buffy Citrine (XVI19'k) to Light Brownish Olive (XXX19"i) at centre, Citrine-Drab (XL19"i), Drab (XLVI17"i) to Benzo Brown (XLVI13"i) when mature, often turning Buffy Olive (XXX21"i) to Saccardo's Olive (XVI19'm) when old and dry; margin acute to subacute, involute when young, straight with maturity, sometimes dehiscent, undulate to curled-up when old, striate $1/4-1/3$ towards the centre, not or rarely weakly tuberculate, peeling $1/5-1/3$ towards the centre, rarely flaking in small patches, with an ochre tinge of Old Gold (XVI19'i), Olive Ochre (XXX21") to Tawny-Olive (XXIX17"i). *Lamellae* adnate to subadnate, 3–6 mm in height at the midpoint, sometimes forked near the stipe and the pileus edge, interveined, white to pale cream, White (LIII) when young, Light Buff (XV17'f) to Cream Colour (XVI19'f) with age, rarely stained reddish-brown tinge of Buckthorn Brown (XV17'i) when bruised, taste slightly to moderately acrid; edge even, constricted towards the margin, 9–19 pieces per cm at the edge; lamellulae infrequent. *Stipe* central to subcentral, $2.4-9.3 \times 1.3-2.7 \text{ cm}$, slightly narrowing towards the base and apex, smooth at first, longitudinally slightly rugulose when mature, White (LIII) first, sometimes faintly stained with Honey Yellow (XXX19") to Olive Ochre (XXX21") when bruised, stuffed first, fistulous to hollow when old. Context 2–5 mm thick above the stipe, initially White (LIII), unchanging or slowly turning pale ochre tinge of Cinnamon Buff (XXIX15"d) when bruised, pale greyish-yellow tinge of Cartridge Buff (XXX19"f) at base when old, taste slightly to moderately acrid, with no distinct odour. Spore print cream coloured (Romagnesi IIc–IId).

Basidiospores [250/10/5] $(5.3-5.6-7 (-7.3) \times (4.1-4.6-6 (-6.3) \mu\text{m})$, $Q = (1.02-1.05-1.31 (-1.37) (Q = 1.19 \pm 0.09)$, $6.3 \times 5.2 \mu\text{m}$ in average, mostly subglobose to broadly ellipsoid, rarely globose and ellipsoid, ornamentation amyloid, composed of long ridges forming an incomplete to complete reticulum, rarely intermixed with an isolated conical to verrucous warts and short crests, $0.3-0.5 \mu\text{m}$ in height; suprahilar spot inamyloid and indistinct. *Basidia* $27-50 \times 8-12 \mu\text{m}$, hyaline in KOH, subcylindrical to subclavate, rarely clavate or subfusiform, inflated towards the upper end or mid-piece, 4-spored, projecting $15-30 \mu\text{m}$ beyond hymenium; sterigmata $3-6 \mu\text{m}$, slightly tortuous, sometimes straight. *Hymenial cystidia* sparsely distributed, fewer than $200/\text{mm}^2$, $56-73 \times 6-12 \mu\text{m}$, fusiform to subclavate, projecting $20-40 \mu\text{m}$ beyond the hymenium, contents granular, sparsely distributed, slightly greyish in SV; apex subacute, rarely obtuse; lamellar edge sterile. *Pileipellis* two layered, composed of suprapellis (80–140 μm thick) and subpellis (100–150 μm thick). Suprapellis an ixotrichoderm,

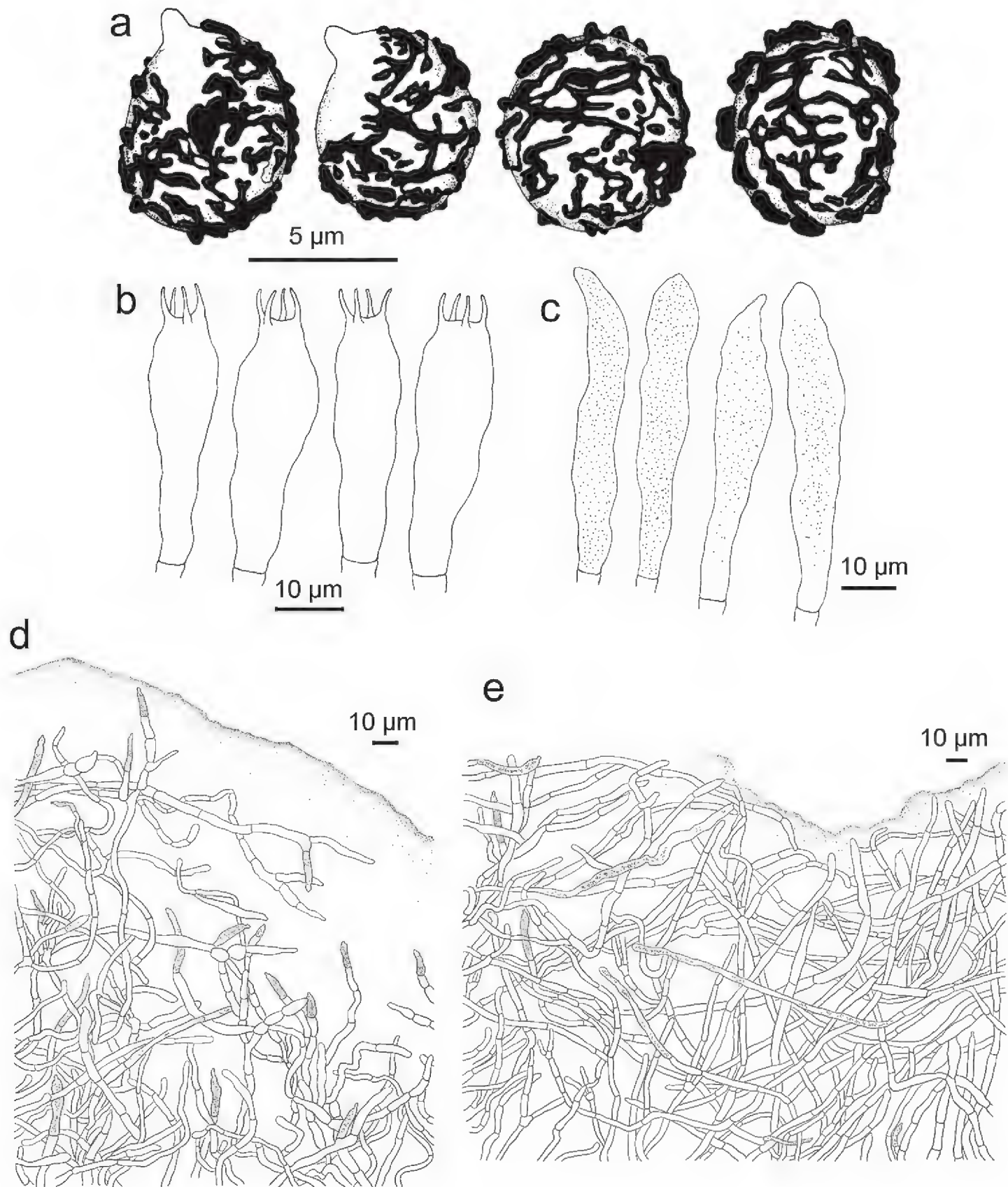


Figure 8. *Russula subpectinatoides*, holotype **A** basidiospores **B** basidia **C** hymenial cystidia **D** suprapellis in pileus centre **E** suprapellis in pileus margin.

composed of gelatinised, ascending to vertical, septate hyphae, acid-resistant encrustations absent, terminal cells mostly lanceolate to bayonet-shaped at pileus centre, mostly tapered at apex, rarely cylindrical, $20\text{--}30 \times 4\text{--}7 \mu\text{m}$, subapical cells sometimes inflated, barrel-shaped, ellipsoid or almost subglobose to globose; when compared with suprapellis at pileus centre, its margin is also an ixotrichoderm, but contains more repent elements, $3\text{--}5 \mu\text{m}$ in width, inflated hyphal cells not observed, lateral short ramifications frequent; pileocystidia long, cylindrical, non-septate, $3\text{--}5 \mu\text{m}$ in width,

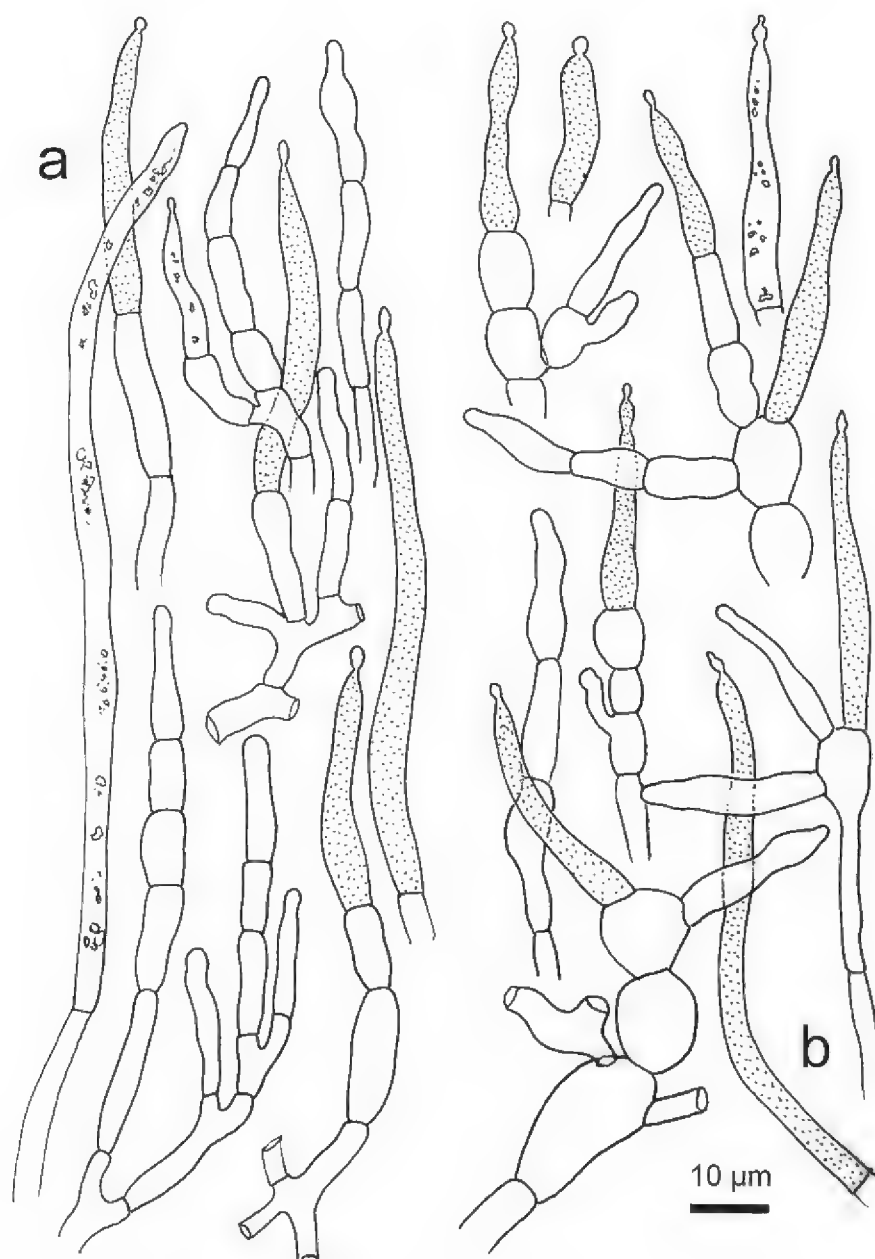


Figure 9. *Russula subpectinatoides*, holotype **A** hyphal extremities in pileipellis margin **B** hyphal extremities in pileus centre.

apex mucronate, contents granulate, sparse, pale grey in SV. Subpellis *a* composed of cylindrical, sometimes inflated, septate, loosely intricate, gelatinous, hyaline hyphae 3–6 µm in width. *Clamp connections* absent in all parts.

Additional specimens examined. China, Jiangsu Province, Nanjing City, Qixia District, Nanjing Normal University, 32°06'N, 118°54'E, alt. 84 m, on the ground in coniferous forest, 28 August 2018, Q.B. Sun 2018002 (HBAU15031, paratype); ibid, 2018003 (HBAU15032, paratype); ibid, 2018004 (HBAU15033, paratype).

Habit and habitat. Single to scattered on yellow brown soil in coniferous forest of subtropical monsoon climate zone dominated by *Cedrus deodara*, *Pinus parviflora* and *P. thunbergii*.

Distribution. China (Jiangsu).

Notes. This new species is similar to *R. pseudopectinatoides* in its brownish-yellow pileus, slightly acrid taste, cream spore print, spores with low, subreticulate ornamentation and gelatinous pileipellis. It is notable that basidiomata of *R. subpectinatoides* were collected from a forest of introduced coniferous tree species. *Cedrus deodara* is native in the western Himalayas, while *Pinus parviflora* and *P. thunbergii* are naturally distrib-

uted in the Japanese archipelago and Korean peninsula. Therefore, this new taxon may also occur in these introduced areas with its accompanying trees.

The Asian species of sect. *Ingratae* already recognizable by their long slender stipe, such as *R. gelatinosa*, *R. guangdongensis*, *R. punctipes*, *R. senecis*, *R. subpunctipes* and *R. tsokae* and cannot be confused with our new species, even more so because they have basidiospores composed of long wings, 2 μm high or more (Song et al. 2018, 2020). A similarly-winged spore ornamentation also differentiates species of the *R. grata* lineage which, moreover, usually have a distinct bitter almond smell. The more golden yellow pileus of species in the *R. foetens* or *R. subfoetens* lineages also avoids confusion with our new species and because many of these are distinctly very acrid. The strong yellowish stipe base that turns immediately red with KOH easily allows one to distinguish the few species of the *R. insignis* lineage. In the *R. granulata* lineage, the Asian species *R. rufobasalis* has reddish tinged stipe base, pleurocystidia with mucronate or appendiculate apices and longer terminal cells, up to 60 μm (Song et al. 2018). Finally, the typically very acrid taste allows us to eliminate most species of the *R. amoenolens* lineage, notwithstanding their sometimes quite similar colouration. The same very acrid taste also differentiates *R. obscuricolor*, which was described from the Indian Himalayas (Das et al. 2017) and showed close affinity to some Southern Hemisphere *Ingratae* in our phylogeny.

After application of these criteria, we are principally left with the phylogenetically closer species of the *R. praetervisa* lineage as potential sources of confusion, most of which are mild to merely slightly acrid. From Asia, this concerns essentially *R. pseudopectinatoides*, a species that can be distinguished by its larger basidiospores (6–) 6.5–9 (–9.5) \times 5–7.5 (–8) μm , hymenial cystidia sometimes with moniliform or capitate appendages and terminal cells of pileipellis with obtuse to ventricose apices (Li et al. 2015b); *R. abmadii* differs in small basidiomata with pileus 1–4.5 cm in diam. and pileipellis a cutis with bifurcated terminal cells (Jabeen et al. 2017). The European species *R. recondita* Melera & Ostellari has a fruity-acidic, but overall unpleasant context smell, larger basidiospores 7–8.5 \times 5.5–7 μm , with ornamentation composed of mostly isolated obtuse conical warts up to 1 μm high (Melera et al. 2017). From North America, *R. amerorecondita* Avis & Barajas has a strongly tuberculate-striate pileus margin, white to pale cream spore print, larger basidiospores (6.5–) 7.1–7.6–8.1 (–9.5) \times (5–) 5.6–6.3–6.9 (–8) μm with more isolated ornamentation and a habitat in hardwood forest dominated by *Quercus*; *R. garyensis* Avis & Barajas has context with unpleasant, bleachy, fishy to parmesan smell, higher basidiospore ornamentation (0.6–) 0.8–1 (–1.4) μm , longer hymenial cystidia (62–) 71.5–81.4–91 (–103) \times 7–8.1–9 (–10) μm and apex sometimes with two, long, usually narrow appendages (Adamčík et al. 2019).

***Russula succinea* G.J. Li & C.Y. Deng, sp. nov.**

Figs 2e, 2f, 3d, 10 and 11.

Fungal Names: FN 570760

Etymology. referring to the pale brownish tinged pileus.

Holotype. China, Guizhou Province, Weining Yi, Hui, and Miao Autonomous County, Caohai National Nature Reserve, 26°53'N, 104°12'E, alt. 2183 m, on the ground in coniferous forest, 15 July 2017, C.Y. Deng CH2017071509 (HGAS-MF 009904, **Holotype**). GenBank accession: MN649188 (ITS).

Diagnosis. This species is characterised by the yellowish-brown to pale brown pileus, with tuberculate-striate margin, adnate and pale cream-coloured lamellae, subclavate to subcylindrical stipe turning cream to pale ochre when bruised, white context unchanging after injury, slightly acrid to mild taste, pale cream spore print, globose, subglobose to broadly ellipsoid basidiospores $(5.8-6.1-7.8 (-8.3) \times (4.9-5.2-6.8 (-7.3) \mu\text{m}$, $7.0 \times 6.0 \mu\text{m}$ on average, ornamentation $0.8-1.2 \mu\text{m}$ in height, forming incomplete reticulum, rarely intermixed with isolated warts, clavate to subcylindrical basidia, $44-66 \times 10-12 \mu\text{m}$, fusiform hymenial cystidia $71-88 \times 9-15 \mu\text{m}$, two-layered pileipellis, ixotrichodermal suprapellis in pileus centre, a trichoderm at the margin, subpellis a cutis and habitat in coniferous forests.

Description. *Basidiomata* small to medium sized. *Pileus* 32–54 mm in diam., initially hemispherical, then plano-convex, flat when mature, often slightly depressed at centre, strongly viscid when wet, yellowish-brown tinged, pale brownish tinged, often intermixed with greyish-yellow fringe, Hazal (XIV11'k), Russet (XV13'k), Cinnamon Brown (XV15'k) to Tawny (XV15') at centre, rarely with Liver Brown (XIV17'm), Pecan Brown (XXVIII13'i) or Rood's Brown (XXVIII11'k) when old and dry; margin subacute to acute, straight, rarely split or inward-turned, tuberculate-striate 14–25 mm from the edge inwards, peeling 1/3–1/2 towards the centre, pale yellowish tinged, first Deep Colonial Buff (XXX21''b), Honey Yellow (XXX19'') to Light Ochraceous Salmon (XV13'd), then Light Cadmium (IV19), Maize Yellow (III19f) when mature. *Lamellae* adnate, 3–6 mm in height at the halfway point of pileus radius, brittle, often forked near the stipe and pileus edge, interveined, pale cream-coloured, first White (LIII), Cream Colour (XVI19'f) when mature, sometimes stained with Martius Yellow (III23f) to Baryta Yellow (IV21f); edge entire, narrowing towards the pileus margin, 13–22 pieces per cm in the edge; lamellulae absent. *Stipe* slightly subcentral, rarely central, $4.2-8.3 \times 1.5-2.2 \text{ cm}$, subclavate to subcylindrical, often narrowing towards the base, rarely slightly curved, smooth when young, rugulose longitudinally in age, dry, Cream Colour (XVI19'f), staining Sudan Brown (III15k) to Orange-Citrine (IV19k) when bruised, Tawny Olive (XXIX17'i), Sayal Brown (XXIX15'') to Isabella Colour (XXX19'i) at base, initially solid, turning hollow in age. Context White (LIII), unchanging when bruised or touched, 3–5 mm thick at the centre of pileus, fragile, taste first slightly acrid, mild when mature, odour indistinct. *Spore print* pale cream (Romagnesi IIc–IIId).

Basidiospores [350/14/7] $(5.8-6.1-7.8 (-8.3) \times (4.9-5.2-6.8 (-7.3) \mu\text{m}$, $Q = (1.00-1.03-1.30 (-1.33) (Q = 1.17 \pm 0.08)$, $7.0 \times 6.0 \mu\text{m}$ on average, globose, subglobose to broadly ellipsoid, rarely ellipsoid, composed of verrucous to subcylindrical amyloid warts $0.8-1.2 \mu\text{m}$ in height, often linked as short to long crests and ridges, forming an incomplete reticulum, rarely intermixed with isolated warts; suprahilar spot distinct, but not amyloid. *Basidia* $44-66 \times 10-12 \mu\text{m}$, mostly 4-spored, clavate to subcylindrical; sterigmata $4-6 \mu\text{m}$ in length, straight to tortuous. *Hymenial cys-*

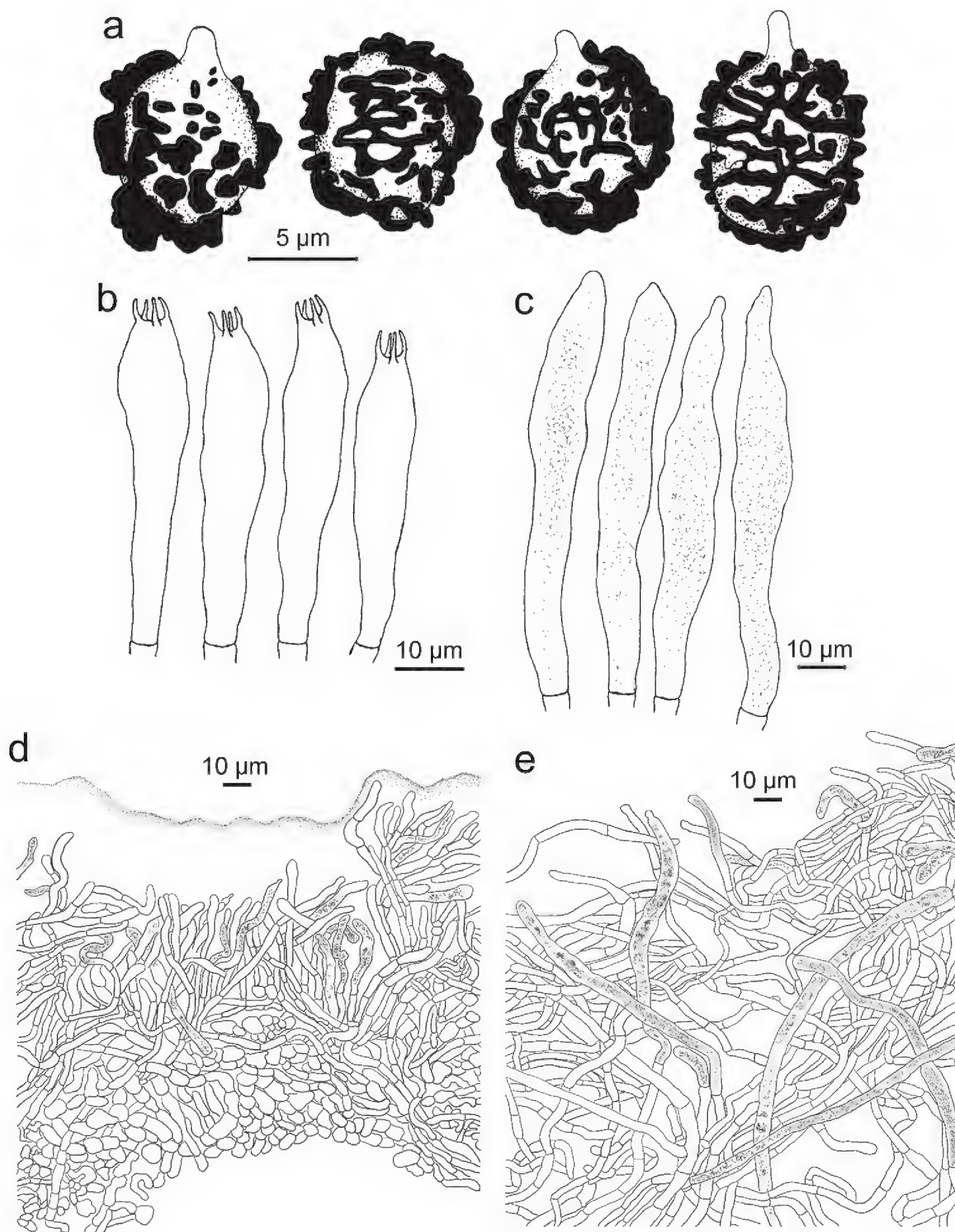


Figure 10. *Russula succinea*, holotype **A** basidiospores **B** basidia **C** hymenial cystidia **D** suprapellis partial subpellis in pileus centre **E** suprapellis in pileus margin.

tidia moderately numerous, ca. 700–1300/mm², 71–88 × 9–15 µm, fusiform, sometimes cylindrical, thin-walled, apex obtuse, rarely mucronate, projecting 20–40 µm beyond the hymenium, contents granular to crystalline, partly dense, blackish-grey

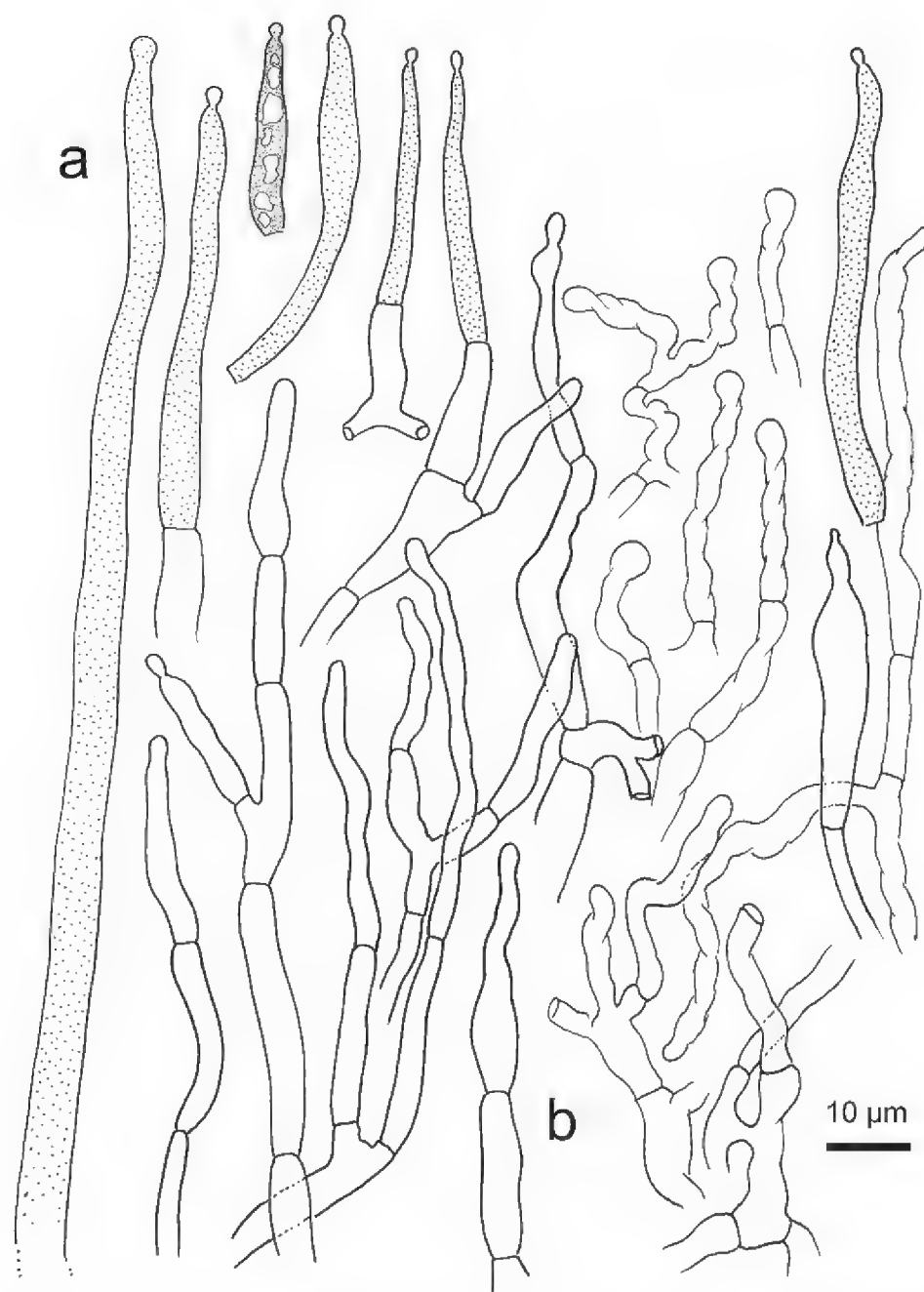


Figure 11. *Russula succinea*, holotype **A** hyphal ends in pileipellis margin **B** hyphal ends in pileus centre.

in SV. *Pileipellis* two-layered, distinctly delimited from the underlying context. The upper suprapellis (70–130 µm thick) in pileus centre an ixotrichoderm, composed of ascending to erect hyphae 4–7 µm in width, septate, cylindrical, often slightly inflated, acid-resistant encrustations absent, terminal cells sometimes narrowing towards the apex, subapical cells cylindrical, not branched; suprapellis a trichoderm in pileus margin, composed of repent, slender, cylindrical, hyaline hyphae 3–5 µm in width, acid-resistant encrustations absent. *Pileocystidia* abundant, long, cylindrical, often septate, 4–10 µm in width, apex obtuse, contents granulate, dense, blackish-grey in SV. The lower layer subpellis (50–90 µm thick) composed of loosely interwoven, mostly repent, cylindrical, septate hyaline hyphae often inflated, 2–7 µm in width. *Clamp connections* not observed in all parts.

Additional specimens examined. China, Guizhou Province, Weining Yi, Hui and Miao Autonomous County, Caohai National Nature Reserve, 26°53'N, 104°12'E, alt. 2215 m, on the ground in coniferous forest, 16 July 2017, C.Y. Deng CH2017071602 (HGAS-MF 009915, paratype); *ibid*, alt. 2136 m, 15 July 2017, C.Y. Deng dcy2307

(HGAS-MF 009909, paratype); *ibid*, alt. 2005 m, C.Y. Deng dcy2309 (HGAS-MF 009906, paratype); alt. 2057 m, C.Y. Deng dcy2308 (HGAS-MF 009902, paratype); alt. 2103 m, C.Y. Deng dcy2304 (HGAS-MF 009914, paratype); Jiangxi Province, Jiujiang City, Lushan City, Lushan Mountains, alt. 1257 m, on the ground in coniferous forest, 19 October 2016, J.B. Zhang (HFJAU 0301).

Habit and habitat. Single to scattered on yellow brown soil in coniferous forest dominated by *Pinus armandii*, *P. massoniana* and *P. yunnanensis* at 1200–2200 m altitude.

Distribution. China (Guizhou and Jiangxi).

Notes. This new species is reminiscent of *R. foetentula*, *R. obscuricolor* and *R. rufobasalis* because of the reddish-brown or burnt sienna colour at the stipe base (Peck 1907; Song et al. 2018). The following characters are helpful for differentiating these two species from *R. succinea*: *R. foetentula* has lower basidiospore ornamentations 0.5–0.9 μm connected by occasional to rare line connections, hymenial cystidia with mucronate-appendiculate apices 2–7 μm long, pileocystidium apex often constricted to 1–2.5 μm in width; North American distribution (Peck 1907; Adamčík et al. 2013); *R. obscuricolor* has darker brown to chocolate brown tinges at pileus centre, bitter to pungent taste of context and shorter hymenial cystidia (pleurocystidia 30–65 \times 6–9 μm , cheilocystidia 23–33 \times 5–7 μm) (Das et al. 2017); *R. rufobasalis* has bright reddish tinge at stipe base, basidiospore ornamentations 0.3–0.8 μm in height and frequently thick-walled, narrower terminal cells 2–5 μm in width (Song et al. 2018).

For those Asian sect. *Ingratae* members that have similar pileus tinges, *R. ahmadii* can be distinguished from *R. succinea* by lower basidiospore ornamentations up to 0.3 μm , shorter basidia (29–) 29.7–38.9 (–40.1) \times (9.2–) 9.4–11.3 (–11.8) μm and pileipellis a cutis (Jabeen et al. 2017); *R. arunii* differs from the new species in the orange tinge intermixed on pileus surfaces, white spore print, narrow pileocystidia 3–4 μm in width and a habit of broad-leaved *Pterigota alata* forest (Crous et al. 2017); *R. catillus* differs in that basidiospore ornamentation is composed of mostly isolated, verrucous to conical warts, absence of pileocystidia in pileipellis and a habitat of oak hardwood forest (Lee et al. 2017); *R. indocatillus* can be differentiated from the new species for white spore print, shorter basidia 34–40 \times 9–11 μm and capitate hymenial cystidium apex (Ghosh et al. 2020); *R. natarajanii* differs in having light to medium brown spots at the pileus periphery, shorter basidia 28–35 \times 7.5–9 μm and a habitat of *Quercus* forest (Das et al. 2006); *R. pseudocatillus* differs in the presence of lamellula, basidiospores ornamented with isolated warts never forming a reticulum and a habitat of broad-leaved evergreen forest (Yuan et al. 2019); *R. pseudopectinatoides* can be distinguished from the new species in having hymenial cystidia with moniliform or capitate apex, larger basidiospores up to 9 μm in diam. and absence of pileocystidia (Li et al. 2015b); *R. straminella* differs in its shorter basidia and hymenial cystidia, often thick-walled terminal cells in pileipellis of pileus margin (Figs 6 and 7); *R. gelatinosa*, *R. punctipes*, *R. seneicis*, *R. subpunctipes* and *R. tsokae* differ from *R. succinea* in their larger basidiospores (9 μm in diam.) with high ornamentation up to 2 μm in height (Khatua et al. 2015; Lee et al. 2017; Song et al. 2018; 2020).

Discussion

The modern taxonomy of *Russula* calls for a combination of detailed microscopic observations with universal and specific standard, multi-gene phylogenetic analyses and accurate symbiotic plant species information (Buyck et al. 2018; Adamčík et al. 2019). The ITS phylogenetic analyses are the most common for practical identification of *Russula* species, because ITS is regarded as an adequate single gene DNA barcode for this genus (Li et al. 2019) and it has the largest number of available referential sequences in open databases (Schoch et al. 2012). A combination of morphological and ITS phylogenetic analyses supported the three new species amongst Asian *Ingratae*: *R. straminella*, *R. subpectinatoides* and *R. succinea*. The results of this study also indicate that *R. indocatillus* may have a wider distribution, from the Himalayan region to south-western China. The four species discussed here have distinct morphologies that allow each one to be differentiated from the others:

- *R. subpectinatoides* and *R. indocatillus* possess the more or less inflated, short-celled chains of hyphal ends, typical for most species in the subgenus *Heterophyllidia* (Figs 4, 5, 8 and 9). These are abundant in *R. subpectinatoides*, but less so in *R. indocatillus* and absent in both other species which possess very dense, intricate and strongly branching, narrow ends in the pileipellis, more or less cemented in mucus that make microscopic examination of these hyphal ends very difficult. Compared to *R. straminella*, hyphal ends in the pileus centre of *R. succinea* have a more wavy-undulate form (Figs 6, 7, 10 and 11).

All four species have similar pileocystidia, but in *R. indocatillus*, they are smaller overall at the pileus surface compared to the other three species (Figs 4 and 5), while in *R. straminella*, they are often more or less thick-walled (Figs 6 and 7).

When comparing basidiospores, *R. subpectinatoides* stands out because of the low subreticulate ornamentation (Figs 3 and 8), whereas the other species have more developed, higher warts or ridges that are much less interconnected, while *R. indocatillus* has almost completely isolated warts (Figs 3 and 4).

Some European members of section *Ingratae*, viz. *R. amoenolens* Romagn., *R. pectinata* Fr., *R. pectinatoides* Peck and *R. sororia* (Fr.) Romell may have been confused morphologically with some of these new species (Wu 1989; Ying and Zang 1994), but more recent diversity analyses indicated that some Chinese specimens, identified as *R. amoenolens* and *R. insignis* Quél., have broad morphological similarities, but also considerable difference (ca. 2%) in the ITS sequence compared to European samples of these species (Li 2014; Liu et al. 2017; Cao et al. 2019). Whether these Chinese specimens represent unknown taxa or intraspecific geographically-separated populations is still debatable (Wang 2020). The factual presence of these species of European and North American origin in China have been analysed in recent years (Li 2014; Zhang 2014; Wang 2019; Liu 2019) and symbiotic host plants were found to be very similar between north-eastern China, Europe and North America (Wu 1979).

The topology of the ITS phylogram (Fig. 1) in this study largely corresponds to that of Park et al. (2017). Of the three subsections in sect. *Ingratae*, the majority of subsect. *Pectinatinae* Bon (type species *R. pectinata*) with species that are typically more greyish-brown to greyish-cream is distributed over clades C and H (Bon 1988), while *Subvelatae* (Singer) Singer (type species *R. subvelata* Singer) with members that have velar rudiments consisting of loosely, arachnoid-pulverulent floccons on pileus surface (Singer 1986), forms the highly-supported clade I. The species *R. indocatillus*, newly-recorded from China in this study, is located in Clade H. This well-supported clade also contains the *R. amoenolens* complex from Europe and *R. cerolens* and allies from North America. The African species complex of *R. oleifera* Buyck in subsect. *Oleiferinae* Buyck (type species *R. oleifera* Buyck) with species that sometimes present an annulus, corresponds to Clade D (Sanon et al. 2014). This clade was a sister clade to the remainder of sect. *Ingratae* in the multilocus phylogenetic analysis of Buyck et al. (2018). The large majority of European species that cluster around *R. foetens* compose clade F, a clade highly supported by Bayesian analysis only. The latter clade is typically composed of yellowish-brown to orange brown species and roughly corresponds to species traditionally placed in subsect. *Foetentinae* (Melzer & Zvara) Singer (type species *R. foetens*), of which it is characterised by dull, ochraceous or pallid coloured pileus, often with pectinate-sulcate to tuberculate-sulcate and distinctly subacute to acute margin, context odour of nitrobenzene, oily, fish, iodoform, or of other unpleasant smells (Singer 1986). Clade F also contains two of our new species, *R. straminella* and *R. succinea*, which share a similar pileipellis structure. Clade E received higher support in ML and MP analyses and shared with Clade F that two of the three species were also yellowish- to orange brown. This clade harbours three species: *R. rufobasalis* from Asia and the North American *R. granulata* Peck and *R. ventricosipes*. The results of our phylogenetic analyses, based on ITS sequences, indicate that more unknown subsections may exist in sect. *Ingratae*. More complex multi-gene analyses are urgently needed to clarify the phylogenetic relationships amongst species in this section.

Compared with previous analyses (Melera et al. 2016; Lee et al. 2017), more gasteroid species of sect. *Ingratae* were included in our study. The majority of gasteroid taxa clustered as two branches in Clade F. The other gasteroid species were mainly scattered in clades of agaricoid taxa. The phylogenetic topologies and low supported branches within sequestrated complex 2 may indicate an urgent need to study the type material of these gasteroid species for clarification of synonyms.

Lee et al. (2017) summarised the general patterns observed for spores in the four clades of sect. *Ingratae* by showing a trend for basidiospore size to increase, while the shape changes from ellipsoid to spherical and for species that have smaller spores to have more ellipsoid spores and vice versa. However, these patterns were less clear when gasteroid species of this section were taken into account (Table 2). These gasteroid species suggest that the patterns, proposed in Lee et al. (2017), do not fit well with all members of the sect. *Ingratae*. Gasteroid taxa are known to have typically more globose and larger spores, because there are no evolutionary pressures of asymmetrical spores with hilar appendages for ballistospory in agaricoid species (Wilson et al. 2011). According to statistics, exceptions that do not follow these general patterns are common in sect. *Ingratae*. Over 40% (5/11) of counted gasteroid species of this section have sub-

Table 2. Spore sizes and shapes of gasteroid sect. *Ingratae* species.

| Species | Spore size (μm) | Spore shape (Q value) | Reference |
|---|--|---|---------------------------------|
| <i>R. ammophila</i> (J.M. Vidal & Calonge) Trappe & T.F. Elliott | 7–9 × 5.5–7.5 | subglobose to broadly ellipsoid | Vidal et al. (2002) |
| <i>Russula aromatica</i> Trappe & T.F. Elliott | 8–11 × 7.5–10 | globose to subglobose | Smith (1963) |
| <i>R. brunneonigra</i> T.Lebel | 11–14(–15) × 11–13(–15) | globose (Q = 1.00–1.03) | Lebel and Tonkin (2007) |
| <i>R. galbana</i> T.Lebel | 8–10 × 8–10 | globose (Q = 1.01–1.06) | Lebel and Tonkin (2007) |
| <i>R. mistiformis</i> (Mattir.) Trappe & T.F. Elliott | (8.5–) 9.5–11 (–12.5) × (8–) 8.5–10 (–10.5) | subglobose to broadly ellipsoid (Q = 1.1–1.2) | Vidal et al. (2019) |
| <i>R. nondistincta</i> (Trappe & Castellano) Trappe & T.F. Elliott | 7–11 in diam. | globose | Trappe and Castellano (2000) |
| <i>R. parksii</i> (Singer & A.H. Sm.) Trappe & T.F. Elliott | 8–11 × 7–9 /10–14(–18) × 9–12(–14) | subglobose to ellipsoid | Singer and Smith (1960) |
| <i>R. pilosella</i> (Cribb) T.Lebel | 8.5–10 × 8–9.5 | subglobose to broadly ellipsoid (Q = 1.07–1.2) | Lebel and Tonkin (2007) |
| <i>R. similaris</i> Trappe & T.F. Elliott | 9–12 × 8–10 | globose to subglobose | Singer and Smith (1960) |
| <i>Russula shafferi</i> Trappe & T.F. Elliott | 8–11 × 8–9 | subglobose to broadly ellipsoid | Singer and Smith (1960) |
| <i>Russula subfulva</i> (Singer & A.H. Sm.) Trappe & T.F. Elliott | 9–12 × 8–11 | globose to subglobose | Singer and Smith (1960) |

globose to broadly ellipsoid, even ellipsoid spores. In simple terms, a significant portion of gasteroid species have larger, but still more ellipsoidal spores. The authors suggested that these exceptions may be ascribed to the multiple and irreversible evolutions of gasteromycetation (Miller et al. 2001; Hibbett 2007). Ancestor genotype, divergence time and environmental factors all may exert different influences on this phenotype.

Spore ornamentations consisting of winged ridges are regarded as one of the most distinctive morphological characters for some members of sect. *Ingratae*. These species include *R. grata*, *R. fragrantissima* and *R. illota* from Europe and northern China, *R. mutabilis* from North America, *R. gelatinosa*, *R. punctipes*, *R. subpunctipes* and *R. senecis* from eastern and southern Asia. A majority of these species and *R. foetens* formed a not highly supported clade in phylogenetic analyses of Lee et al. (2017). As more samplings and species of sect. *Ingratae* were involved, the monophyly of winged-spore species was not supported in this analysis. Close phylogenetic relationships were detected in strongly-supported clades of *R. grata*-*R. fragrantissima*, *R. mutabilis*-*R. illota* and *R. punctipes*-*R. subpunctipes*-*R. senecis*. This phylogenetic inconsistency called for a further multi-gene analysis.

The habitats of the four species of this study show a common feature of coniferous forests dominated by *Pinus* spp. The current altitudes of distributions of *R. indocatillus* and *R. succinea* indicate a habitat of subalpine climate. These two species may have wider distributions than current records because the corresponding ectomycorrhizal symbiotic trees are representative and widespread species in Sino-Japanese and Sino-Himalayan floral subregions (Wu 1980; Chen et al. 2020). For *R. straminella* and *R. subpectinatoides* which were collected from reforested plantations and transplanted botanic gardens, intensive samplings on initial areas of symbiotic trees are needed for clarifying the types of habitats.

Specimens of the four species in this analysis were all collected on yellow brown soil. Local analyses showed high nitrogen conditions in soil environments of these species (Cai et al. 2010; Wang et al. 2010; Zhang et al. 2014). This result supported the conclusions in Avis (2012) that nitrophilic tendencies appear throughout fetid *Russulas*.

Acknowledgements

This work was financially supported by the Science and Technology Support Project of Guizhou Province [(2019) 2451–2, (2018) 4002], Talent Introduction Scientific Research Special Project of Hebei Agricultural University (YJ201849), National Natural Science Foundation of China (Nos. 31500013, 30770013, 31960008), the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment of China (No. 2019HJ2096001006), the Provincial Key Technologies R&D Program of Guizhou [(2017) 2513], the Earmarked Fund for Hebei Edible Fungi Innovation Team of Modern Agro-industry Technology Research System (No. HBCT2018050205), Key Research and Development Planning Project in Science and Technology of Hebei Province (No. 21326315D), Jiangxi Province Department of Education Science and Technology Research Project, (No. GJJ190925), Construction and Application of the main Edible and Medicinal Fungal Resource Information-based Intelligent Platform of Guizhou Province [(2019) 4007] and the Science and Technology Foundation Project of Guizhou Province [(2016) 1153].

References

- Adamčík S, Carteret X, Buyck B (2013) Type studies on some *Russula* species described by C.H. Peck. *Cryptogamie Mycologie* 34(4): 367–391. <https://doi.org/10.7872/crym.v34.iss2.2013.367>
- Adamčík S, Jančovičová S, Buyck B (2018) The *Russulas* described by Charles Horton Peck. *Cryptogamie Mycologie* 39(1): 3–108. <https://doi.org/10.7872/crym/v39.iss1.2018.3>
- Adamčík S, Looney B, Caboň M, Jančovičová S, Adamčíková K, Avis PG, Barajas M, Bhatt RP, Corrales A, Das K, Hampe F, Ghosh A, Gates G, Kälviäinen V, Khalid AN, Kiran M, Lange RD, Lee H, Lim YW, Kong A, Manz C, Ovrebo C, Saba C, Taipale T, Verbeken A, Wisitrassameewong K, Buyck B (2019) The quest for a globally comprehensible *Russula* language. *Fungal Diversity* 99(1): 369–449. <https://doi.org/10.1007/s13225-019-00437-2>
- Avis PG (2012) Ectomycorrhizal iconoclasts: the ITS rDNA diversity and nitrophilic tendencies of fetid *Russula*. *Mycologia* 104: 998–1007. <https://doi.org/10.3852/11-399>
- Bau T, Bao HY, Li Y (2014) A revised checklist of poisonous mushrooms in China. *Mycosystema* 33(3): 517–548. <https://doi.org/10.13346/j.mycosystema.130256>
- Bazzicalupo AL, Buyck B, Saar I, Vauras J, Carmean D, Berbee ML (2017) Troubles with mycorrhizal mushroom identification where morphological differentiation lags behind barcode sequence divergence. *Taxon* 66(4): 791–810. <https://doi.org/10.12705/664.1>
- Bi ZS, Li TH (1986) A preliminary report note on *Russula* species from Guangdong, with a new species and a new variety. *Guihaia* 6(3): 193–199
- Bon M (1988) Clé monographique des russules d'Europe. *Documents Mycologiques* 18 (70–71): 1–120
- Buyck B, Duhem B, Das K, Jayawardena RS, Niveiro N, Pereira OL, Prasher IB, Adhikari S, Albertó EO, Bulgakov TS, Castañeda-Ruiz RF, Hembrom ME, Hyde KD, Lewis DP,

- Michlig A, Nuytinck J, Parihar A, Popoff OE, Ramirez NA, da Silva M, Verma RK, Hofstetter V (2017) Fungal biodiversity profiles 21–30. *Cryptogamie Mycologie* 38(1): 101–146. <https://doi.org/10.7872/crym/v38.iss1.2017.101>
- Buyck B, Zoller S, Hofstetter V (2018) Walking the thin line... ten years later: the dilemma of above- versus below-ground features to support phylogenies in the Russulaceae (Basidiomycota). *Fungal Diversity* 89(1): 267–292. <https://doi.org/10.1007/s13225-018-0397-5>
- Cai XL, Huang XZ, Liao DP (2010) Analysis of chemical properties of farmland soil in Caohai National Nature Reserve. *Inner Mongolia Agricultural Science and Technology* 3: 60–61
- Calonge FD, Martín MP (2000) Morphological and molecular data on the taxonomy of *Gymnomyces*, *Martellia* and *Zelleromyces* (Elasmomycetaceae, Russulales). *Mycotaxon* 76: 9–15
- Cao B, Li GJ, Zhao RL (2019) Species diversity and geographic components of *Russula* from the Greater and Lesser Khinggan Mountains. *Biodiversity Science* 27(8): 854–866. <https://doi.org/10.17520/biods.2019040>
- Chen YF, Zang RG, Yue TX, Zhang YX, Wang XH, Li YD, Li FR, Chen Q (2020) Forest vegetation in China. China Forestry Publishing House, Beijing, 1–799.
- Chen ZH, Yang ZL, Bau T, Li TH (2016) Poisonous mushrooms: recognition and poisoning treatment. Science Press, Beijing, 1–308.
- Crous PW, Wingfield MJ, Burgess TI, Hardy GE, Barber PA, Alvarado P, Barnes CW, Buchanan PK, Heykoop M, Moreno G, Thangavel R, van der Spuy S, Barili A, Barrett S, Cacciola SO, Cano-Lira JF, Crane C, Decock C, Gibertoni TB, Guarro J, Guevara-Suarez M, Hubka V, Kolařík M, Lira CRS, Ordoñez ME, Padamsee M, Ryvarden L, Soares AM, Stchigel AM, Sutton DA, Vizzini A, Weir BS, Acharya K, Aloï F, Baseia IG, Blanchette RA, Bordallo JJ, Bratek Z, Butler T, Cano-Canals J, Carlavilla JR, Chander J, Cheewangkoon R, Cruz RHF, da Silva M, Dutta AK, Ercole E, Escobio V, Esteve-Raventós F, Flores JA, Gené J, Góis JS, Haines L, Held BW, Jung MH, Hosaka K, Jung T, Jurjević Ž, Kautman V, Kautmanova I, Kiyashko AA, Kozanek M, Kubátová A, Lafourcade M, LaSpada F, Latha KPD, Madrid H, Malysheva EF, Manimohan P, Manjón JL, Martín MP, Mata M, Merényi Z, Morte A, Nagy I, Normand AC, Paloi S, Pattison N, Pawłowska J, Pereira OL, Petterson ME, Picillo B, Raj KNA, Roberts A, Rodríguez A, Rodríguez-Campo FJ, Romański M, Ruskiewicz-Michalska M, Scanu B, Schena L, Semelbauer M, Sharma R, Shouche YS, Silva V, Staniaszek-Kik M, Stielow JB, Tapia C, Taylor PWJ, Toome-Heller M, Vabeikhokhei JMC, van Diepeningen AD, Van Hoa N, Van Tri M, Wiederhold NP, Wrzosek M, Zothanzama J, Groenewald JZ (2017) Fungal planet description sheets: 558–624. *Persoonia* 38:240–384. <https://doi.org/10.3767/003158517X698941>
- Dai YC, Zhou LW, Yang ZL, Wen HA, Bau T, Li TH (2010) A revised checklist of edible fungi in China. *Mycosystema* 29(1): 1–21. <https://doi.org/10.13346/j.mycosystema.2010.01.022>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8): e772. <https://doi.org/10.1038/nmeth.2109>
- Das K, Sharma JR (2005) Russulaceae of Kumaon Himalaya. Botanical Survey of India, Ministry of Environment and Forests, Government of India, Kolkata. 167–168
- Das K, Sharma JR, Atri NS (2006) *Russula* in Himalaya 3: a new species of subgenus *Ingratula*. *Mycotaxon* 95: 271–275

- Das K, Putte VDP, Buyck B (2010) New or interesting *Russula* from Sikkim Himalaya (India). *Cryptogamie Mycologie* 31: 373–387. <https://doi.org/10.7872/crym.v32.iss4.2011.365>
- Das K, Atri NS, Buyck B (2013) Three new *Russula* (Russulales) from India. *Mycosphere* 4:722–732. <http://dx.doi.org/10.5943/mycosphere/4/4/9>
- Das K, Ghosh A, Chakraborty D, Li JW, Qiu LH, Baghela A, Halama M, Hembrom ME, Mehmood T, Parihar A, Pencakowski B, Bielecka M, Reczynska K, Sasiela D, Singh U, Song Y, Swierkosz K, Szczesniak K, Uniyal P, Zhang JB, Buyck B (2017) Fungal biodiversity profiles 31–40. *Cryptogamie Mycologie* 38(3): 353–406. <https://doi.org/10.7872/crym/v38.iss3.2017.353>
- Deng CY, Shi LY, Wang J, Xiang Z, Li SM, Li GJ, Yang H (2020) Species diversity of the *Russula virescens* complex “qingtoujun” in southern China. *Mycosystema* 39(9): 1661–1683. <https://doi.org/10.13346/j.mycosystema.200145>
- Eberhardt U (2002) Molecular kinship analyses of the agaricoid Russulaceae: correspondence with mycorrhizal anatomy and sporocarp features in the genus *Russula*. *Mycological Progress* 1: 201–223. <http://dx.doi.org/10.1007/s11557-006-0019-6>
- Felsenstein J (1985) Confidence intervals on phylogenetics: an approach using bootstrap. *Evolution* 39: 783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Ghosh A, Das K, Bhatt RP, Hembrom ME (2020) Two new species of the genus *Russula* from western Himalaya with morphological details and phylogenetic estimations. *Nova Hedwigia*: https://doi.org/10.1127/nova_hedwigia/2020/0588
- Haelewaters D, Dirks AC, Kappler LA, Mitchell JK, Quijada L, Vandegrift R, Buyck B, Pfister DH (2018) A preliminary checklist of fungi at the Boston Harbor Islands. *Northeastern Naturalist* 25(sp9): 45–76. <https://doi.org/10.1656/045.025.s904>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98
- He B, Li Q, Feng T, Liu Y (2019) Research on community characteristics of the forest in Cao-hai National Nature Reserve. *Journal of Henan Agricultural University* 53(5): 783–790.
- He MQ, Zhao RL, Hyde KD, Begerow D, Kemler M, Yurkov A, McKenzie EHC, Raspé O, Kakishima M, Sánchez-Ramírez S, Vellinga EC, Halling R, Papp V, Zmitrovich IV, Buyck B, Ertz D, Wijayawardene NN, Cui BK, Schoutteten N, Liu XZ, Li TH, Yao YJ, Zhu XY, Liu AQ, Li GJ, Zhang MZ, Ling ZL, Cao B, Antonín V, Boekhout T, da Silva BDB, De Crop E, Decock C, Dima B, Dutta AK, Fell JW, Geml J, Ghobad-Nejhad M, Giachini AJ, Gibertoni TB, Gorjón SP, Haelewaters D, He SH, Hodgkinson BP, Horak E, Hoshino T, Justo A, Lim YW, Menolli Jr. N, Mešić A, Moncalvo J, Mueller GM, Nagy LG, Nilsson RH, Noordeloos M, Nuytinck J, Orihara T, Ratchadawan C, Rajchenberg M, Silva-Filho AGS, Sulzbacher MA, Tkalčec Z, Valenzuela R, Verbeken A, Vizzini A, Wartchow F, Wei TZ, Weiß M, Zhao CL, Kirk PM (2019) Notes, outline and divergence times of Basidiomycota. *Fungal Diversity* 99: 105–367. <https://doi.org/10.1007/s13225-019-00435-4>
- Imai S (1938) Studies on the Agaricaceae of Hokkaido. II. *Journal of the Faculty of Agriculture of the Hokkaido Imperial University* 43: 179–378
- Jabeen S (2016) Ectomycorrhizal fungal communities associated with Himalayan cedar from Pakistan. PhD dissertation. University of the Punjab, Lahore. 1–269

- Jabeen S, Razaq A, Niazi ARK, Ahmad I, Grebenc T, Khalid AN (2017) *Russula ahmadii* (Basidiomycota, Russulales), a new species in section *Ingratae* and its ectomycorrhiza from coniferous forests of Pakistan. *Phytotaxa* 321(3): 241–253. <https://doi.org/10.11646/phytotaxa.321.3.2>
- Katoh K, Standly DM (2013) MAFFT Multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Khatua S, Dutta AK, Acharya K (2015) Prospecting *Russula senecis*: a delicacy among the tribes of West Bengal. *PeerJ* 3: e810. <https://doi.org/10.7717/peerj.810>
- Kishino H, Hasegawa M (1989) Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. *Journal of Molecular Evolution* 29: 170–179. <https://doi.org/10.1007/BF02100115>
- Lebel T, Tonkin JE (2007) Australasian species of *Macowanites* are sequestrate species of *Russula* (Russulaceae, Basidiomycota). *Australian Systematic Botany* 20: 355–381. <https://doi.org/10.1071/SB07007>
- Lee H, Park MS, Jung PE, Eimes JA, Seok SJ, Lim YW (2017) Re-evaluation of the taxonomy and diversity of *Russula* section *Foetentinae* (Russulales, Basidiomycota) in Korea. *Mycoscience* 58(5): 351–360. <https://doi.org/10.1016/j.myc.2017.04.006>
- Li GJ (2014) Taxonomy of *Russula* from China. PhD dissertation. Institute of Microbiology, Chinese Academy of Sciences & University of Chinese Academy of Sciences, Beijing. 1–554. <https://doi.org/10.13140/RG.2.2.20380.59522>
- Li GJ, Li SF, Zhao D, Wen HA (2015a) Recent research progress of *Russula* (Russulales, Agaricomycetes): a review. *Mycosystema* 34(5): 821–848. <https://doi.org/10.13346/j.mycosystema.150085>
- Li GJ, Zhao D, Li SF, Wen HA (2015b) *Russula chiui* and *R. pseudopectinatoides*, two new species from southwestern China supported by morphological and molecular evidence. *Mycological Progress* 14(6): 33. <https://doi.org/10.1007/s11557-015-1054-y>
- Li GJ, Zhao RL, Zhang CL, Lin FC (2019) A preliminary DNA barcode selection for the genus *Russula* (Russulales, Basidiomycota). *Mycology* 10(2): 61–74. <https://doi.org/10.1080/21501203.2018.1500400>
- Liu HY (2019) The study on *Russula* species on Taishan. Shandong Agricultural University, Tai'an. 1–111. <https://doi.org/10.27277/d.cnki.gsdnu.2019.000008>
- Liu XL, Bau T, Wang XH (2017) Species diversity of *Russula* from the Greater and Lesser Hinggan Mountains in Northeast China. *Mycosystema* 36(10): 1355–1368. <https://doi.org/10.13346/j.mycosystema.170015>
- Looney BP, Ryberg M, Hampe F, Sánchez-García M, Matheny PB (2016) Into and out of the tropics: global diversification patterns in a hyperdiverse clade of ectomycorrhizal fungi. *Molecular Ecology* 25(2): 630–647. <https://doi.org/10.1111/mec.13506>
- Looney BP, Meidl P, Piatek MJ, Miettinen O, Martin FM, Matheny PB, Labbé JL (2018) Russulaceae: a new genomic dataset to study ecosystem function and evolutionary diversification of ectomycorrhizal fungi with their tree associates. *New Phytologist* 218(1): 54–65. <https://doi.org/10.1111/nph.15001>
- Melera S, Ostellari C, Roemer N, Avis, PG, Tonolla M, Barja F, Narduzzi-Wicht, B (2017) Analysis of morphological, ecological and molecular characters of *Russula pectinatoides*

- Peck and *Russula praetervisa* Sarnari, with a description of the new taxon *Russula recondite* Melera & Ostellari. *Mycological Progress* 16 (2): 117–134. <https://doi.org/10.1007/s11557-016-1256-y>
- Miller SL, Buyck B (2002) Molecular phylogeny of the genus *Russula* in Europe with a comparison of modern infrageneric classifications. *Mycological Research* 106(3): 259–276. <https://doi.org/10.1017/S0953756202005610>
- Nakamura T, Yamada KD, Tomii K, Katoh K (2018) Parallelization of MAFFT for large-scale multiple sequence alignments. *Bioinformatics* 34(14): 2490–2492. <https://doi.org/10.1093/bioinformatics/bty121>
- Nylander JAA (2004) MrModelTest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University. 1–2
- Peck CH (1907) New York species of *Russula*. *Bulletin of the New York State Museum of Natural History* 116: 67–98
- Razaq A, Ilyas S, Khalid AN, Niazi AR (2014) *Russula foetentoides* (Russulales, Russulaceae)—a new species from Pakistan. *Sydowia* 66(2): 289–298. [https://doi.org/10.12905/0380.sydowia66\(2\)2014-0289](https://doi.org/10.12905/0380.sydowia66(2)2014-0289)
- Ridgway R (1912) Color standards and color nomenclature. Robert Ridgway, Washington, 1–270. <https://doi.org/10.5962/bhl.title.144788>
- Romagnesi H, 1985. Les Russules d'Europe et d'Afrique du Nord. Reprint with supplement. J.Cramer, Lehre, 1–1030.
- Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP, (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Sanon E, Guissou KML, Yorou NS, Buyck B (2014) Le genre *Russula* au Burkina Faso (Afrique de l'Ouest): quelques espèces nouvelles de couleur brunâtre. *Cryptogamie Mycologie* 35(4): 377–397. <https://doi/10.7872/crym.v35.iss4.2014.377>
- Sarnari M (1998) Monografia illustrata de genere *Russula* in Europa. Tomo Primo. AMB, Centro Studi Micologici. Trento, 1–800.
- Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. *Proceedings of the National Academy of Sciences of the United States of America* 109: 6241–6246. <https://doi.org/10.1073/pnas.1117018109>
- Shaffer RL (1972) North American russulas of the subsection *Foetentinae*. *Mycologia* 64(5): 1008–1053. <https://doi.org/10.2307/3758072>
- Singer R (1935) Supplemente zu meiner monographie der gutting *Russula*. *Annales Mycologici* 33: 297–352.
- Singer R, Smith AH (1960) Studies on secotiaceous fungi IX the astrogastreaeous series. *Memoirs of the Torrey Botanical Club* 21(3): 1–112. <https://doi.org/10.2307/43392224>
- Singer R (1986) The Agaricales in modern taxonomy. 4th Ed. Koeltz Scientific Books, Königstein, 1–981.
- Silvestro D, Michalak I (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity and Evolution* 12: 335–337. <https://doi.org/10.1007/s13127-011-0056-0>

- Smith AH (1963) New astrogastreaous fungi from the Pacific Northwest. *Mycologia* 55(4): 421–441. <https://doi.org/10.2307/3756337>
- Song B, Li TH, Wu XL, Li JJ, Shen YH, Lin QY (2007) Known species of *Russula* from China and their distribution. *Journal of Fungal Research* 5(1): 20–42. <https://doi.org/10.13341/j.jfr.2007.01.007>
- Song J, Chen B, Liang JF, Li HJ, Wang SK, Lu JK (2020) Morphology and phylogeny reveal *Russula subpunctipes* sp. nov., from southern China. *Phytotaxa* 459(1): 16–24. <https://doi.org/10.11646/phytotaxa.459.1.2>
- Song Y, Buyck B, Li JW, Yuan F, Zhang ZW, Qiu LH (2018) Two novel and a forgotten *Russula* species in sect. *Ingratae* (Russulales) from Dinghushan Biosphere Reserve in southern China. *Cryptogamie Mycologie* 39(3): 341–357. <https://doi.org/10.7872/crym/v39.iss3.2018.341>
- Swofford DL (2004) PAUP*: phylogenetic analysis using parsimony and other methods. Version 4.0b10. Sinauer, Sunderland.
- Trappe JM, Castellano MA (2000) New sequestrate Ascomycota and Basidiomycota covered by the Northwest Forest Plan. *Mycotaxon* 75: 153–179.
- Vidal JM, Calonge FD, Martin MP (2002) *Macowanites ammophilus* (Russulales) a new combination based on new evidence. *Revista Catalana De Micologia* 24: 69–74.
- Vidal JM, Alvarado P, Loizides M, Konstantinidis G, Chachuła P, Mleczko P, Moreno G, Vizzini A, Krakhmalnyi M, Paz A, Cabero J, Kaounas V, Slavova M, Moreno-Arroyo B, Llistosella J (2019) A phylogenetic and taxonomic revision of sequestrate Russulaceae in Mediterranean and temperate Europe. *Persoonia* 42: 127–185. <https://doi.org/10.3767/persoonia.2019.42.06>
- Wang J, Buyck B, Wang XH, Tolgor B (2019) Visiting *Russula* (Russulaceae, Russulales) with samples from southwestern China finds one new subsection of *R.* subg. *Heterophyllidia* with two new species. *Mycological Progress* 18(6): 771–784. <https://doi.org/10.1007/s11557-019-01487-1>
- Wang JM, Lu ZH, Wu JF, Xiao QL, Zhu MY, Wang HH (2010) The characteristics and distribution patterns of soil types in Mt Lushan. *Acta Agriculturae Universitatis Jiangxiensis* 32(6): 1284–1290. <https://doi.org/10.13836/j.jjau.2010223>
- Wang XH (2020) Taxonomic comments on edible species of Russulaceae. *Mycosystema* 39(9): 1617–1639. <https://doi.org/10.13346/j.mycosystema.200209>
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenies. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) *PCR protocols, a guide to methods and applications*. Academic, San Diego, 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Wilson AW, Binder M, Hibbett DS (2011) Effects of gasteroid fruiting body morphology on diversification rates in three independent clades of fungi estimated using binary state speciation and extinction analysis. *Evolution* 65(5): 1305–1322. <https://doi.org/10.1111/j.1558-5646.2010.01214.x>
- Wisitrassameewong K, Park MS, Lee H, Ghosh A, Das K, Buyck B, Looney BP, Caboň M, Adamčík S, Kim C, Kim CS, Lim YW (2020) Taxonomic revision of *Russula* subsection *Amoeninae* from South Korea. *Mycosystema* 75: 1–29. <https://doi.org/10.3897/mycokeys.75.53673>
- Wu XL (1989) *The macrofungi from Guizhou, China*. Guizhou People's Publishing House, Guiyang, 1–198.

- Wu ZY (1979) The regionalization of Chinese flora. *Acta Botanica Yunnanica* 1(1): 1–22.
- Wu ZY (1980) The Vegetation of China. Beijing: Science Press, Beijing, 1–1375.
- YingJZ, ZangM (1994) Economic macrofungi from southwestern China. Science Press, Beijing, 1–400.
- Yuan F, Song Y, Buyck B, Li JW, Qiu LH (2019) *Russula viridicinnamomea* F. Yuan & Y. Song, sp. nov. and *R. pseudocatillus* F. Yuan & Y. Song, sp. nov., two new species from southern China. *Cryptogamie Mycologie* 40(4): 45–56. <https://doi.org/10.5252/cryptogamie-mycologie2019v40a4>
- Zhang H, Wang XK, Xu JP, Zhang YC, Ai YC (2014) Distribution characteristics of soil carbon and nitrogen and its influencing factors in different farming regions of Jiangsu Province. *Jiangsu Journal of Agricultural Sciences* 30(5): 1028–1036. <https://doi.org/10.3969/j.issn.1000-4440.2014.05.017>
- Zhang X (2014) Researches on taxonomy of some species in *Russula* from China and phylogeny of the genus. Southwest Forestry University, Kunming, 1–72.

Supplementary material 1

Fasta file for phylogenetic analyses

Authors: Guo-Jie Li

Data type: phylogenetic data

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Supplementary material 2

Phylip file for ML analysis

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Data type: phylogenetic

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Supplementary material 3

Nexus file for Bayesian analysis

Authors: Guo-Jie Li

Data type: phylogenetic

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Supplementary material 4

Nexus file for MP analysis

Authors: Guo-Jie Li

Data type: phylogenetic

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